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THE SELECTIVE SIGNIFICANCE OF THE SEX RATIO

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INTRODUCTION

Whether the sex ratio is adjusted by natural selection is a question nearly as old as the concept of selection itself. The difficulty lies in supplying a satisfactory explanation of how selection might operate. According to the conventional view a trait is at a selective advantage only when it leads to the production of a greater than average number of offspring. It follows that any trait such as the sex ratio which does not affect the total number of offspring can have no selective significance.

Evidently a different type of selection must be considered, and this is done in the two schemes which have been offered. Darwin in "The Descent of Man" suggests that a particular sex ratio may be of advantage to the group rather than to the individual. Such intergroup selection is probably in certain instances quite important, but we will consider a different aspect of the problem.

Fisher (1930) shows that parental care of the young may be expected to influence the sex ratio. The implication of his treatment is that unless parental care is involved the primary sex ratio will be 1:1. In this respect the result is similar to our findings, but Fisher's treatment is phrased in non-genetical terms and does not lend itself to further development.

In a later review on the sex ratio Crew (1937) supposes that in man the sex ratio is adjusted so as to be 1:1 for the age group just entering the reproductive stage, although no suggestion is given as to how this might come about.

VARIABILITY OF THE SEX RATIO

Any explanation of how the sex ratio is adjusted assumes that the sex ratio is variable; that the probability of a male is not always 0.5. While more information is needed on this subject, it is known that there is some variability of this sort under the control of genes.

The best known example of a sex ratio gene is "sex ratio" which occurs in certain species of Drosophila. (For literature see Novitski, 1947.) This

gene is sex linked and causes males carrying it to produce nearly exclusively daughters. Novitski found a comparable condition in *Drosophila affinis* resulting in only sons. In this case an autosomal gene was involved as well as one of the sex-linked variety.

POPULATION BEHAVIOR OF AUTOSOMAL SEX RATIO GENES

Assuming that an adequate genetic variability of the sex ratio is available we will consider the role of autosomal genes in its adjustment.

The question to be answered may be posed as follows. Is it possible that the genetic contribution which an individual makes to the following generations is a matter not only of progeny size, but also of the sex ratio of the progeny? The argument for such an idea is developed below and differs from the usual view on this subject in that the transmission of genes is considered not for one, but for two generations.

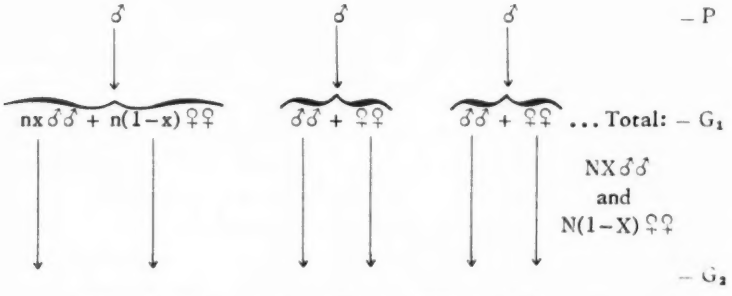

FIGURE 1. The generations P, G_1, and G_2 and their components.

Consider a population in which a male parent produces a progeny of n zygotes, where a progeny is defined as all the offspring of one individual. In any progeny of this kind the probability of a male zygote is x; that of a female zygote $1 - x$. The expected number of male zygotes in the progeny is xn, and the expected number of female zygotes $(1 - x)n$. This progeny together with numerous others makes up the generation G_1 which, together with the preceding and following generations, is shown diagrammatically in figure 1. All the progenies make up a total of N zygotes with a frequency of X males and $1 - X$ females.

Taking a male in the P generation, we would like to know what will be his expected genetic contribution to the G_2. It will turn out that this value, which may be called C_m, depends on the sex ratio of the progeny. The expression to be derived gives C_m as a function of the sex ratio of the progeny, C_m being a measure of genetic contribution to be defined more precisely later. Instead of starting with a male in the P generation, a female could be used and a value C_f, the contribution of a female, could be found. The ensuing treatment can be applied to females equally as well as to males, although the males will be taken for illustration.

As a first step it is necessary to compute the contribution of the progeny to G_2. Consider the males. There are NX males in the G_1 and all together they will supply half the genes which are transmitted from G_1 to G_2. The average contribution of a single male is thus $\frac{1}{2} \cdot 1/NX$.

In a given progeny there are nx males each contributing 1/2NX which makes a total of $\frac{nx}{2NX}$. On the same reasoning the females of the progeny contribute $\frac{n(1-x)}{2N(1-X)}$.

The males and the females together, which is to say the whole progeny, contribute

$$\frac{n}{2N}\left(\frac{x}{X} + \frac{1-x}{1-X}\right) \quad \ldots\ldots (1)$$

Of this fraction of genes contributed by the progeny to the G_2 half come from the male parent of the progeny, and the other half from his mate or mates; and the contribution of the P male is just half that of the progeny:

$$C_m = \frac{n}{4N}\left(\frac{x}{X} + \frac{1-x}{1-X}\right) \quad \ldots\ldots (2)$$

C_m can now be defined as the expected fraction of genes going from P to G_2 contributed by a single male in P.

If we consider a gene which causes the males carrying it to produce male zygotes with a frequency of x, the above expression will tell us something about the effect this condition has on fitness. If X = 0.5 then

$$C_m = \frac{n}{2N}$$

so that the contribution is the same regardless of the value of x. This is to say that any sex ratio is as fit as any other, providing the number of zygotes is independent of the sex ratio. This can be seen in figure 2 where C_m is the same for any value of x in a population of X = 0.5. It can also be seen that for other values of X this is not the case. Take any two values of x, x_1 and x_2. For some values of X, individuals producing a ratio of x_1 will have a higher contribution than those producing x_2; consequently the gene or genes responsible for the ratio x_1 will increase in frequency. For other value of X the reverse is true. The gene or genes favored are always those whose increase will shift the population sex ratio (X) toward 0.5.

This may be seen in a different way by altering formula (2), a procedure which will perhaps make other features clearer. This can be rewritten

$$C_m = \frac{1}{4}\left(\frac{nx}{NX} + \frac{n(1-x)}{N(1-X)}\right)$$

or

$$C_m = \frac{1}{4}\left(\frac{m}{M} + \frac{f}{F}\right)$$

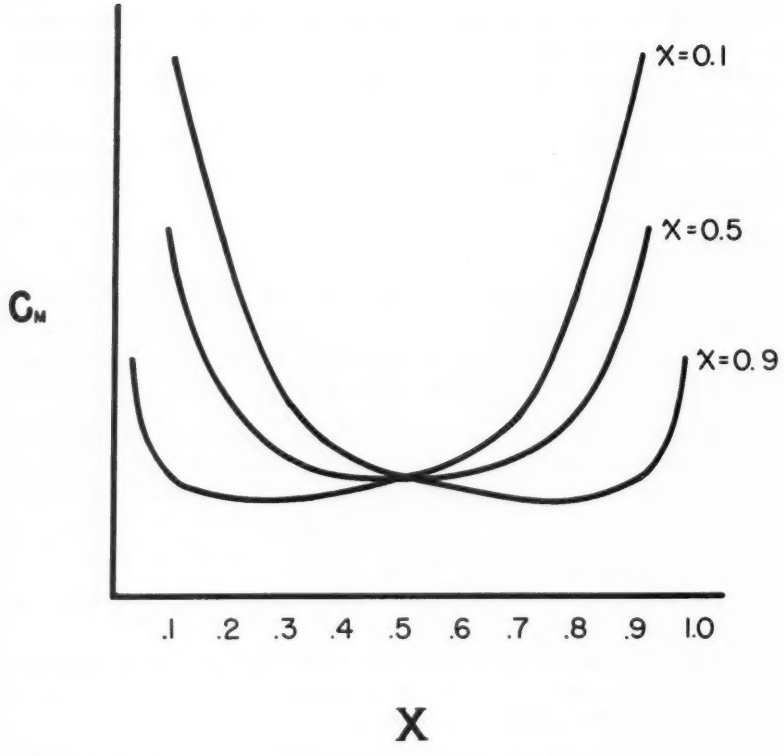

FIGURE 2. Genetic contribution of a male as related to x, the sex ratio of his progeny, and to X, the sex ratio of the population.

where m and f are the numbers of male and female zygotes in the particular progeny while M and F stand for the corresponding numbers in the entire G_1. If F is large relative to M each male in the G_1 will produce a high number of offspring. This is to say that the individual male transmits more genes than the individual female. Consequently the contribution of a particular G_1 progeny, and hence also of the male parent of this progeny, is greater when m is larger than f.

The sex ratio referred to is the primary sex ratio, a fact which can be shown in the following way. Suppose that a male zygote in G_1 has a probability s_1 and a female zygote a probability of s_2 of surviving to adulthood. An expression comparable to formula (1) can be written, but employing nxs_1 and $n(1-x)s_2$, the number of *adult* males and females in the progeny. The contribution of an individual male is then $\frac{1}{2NXS_1}$ and of a female $\frac{1}{2N(1-X)S_2}$. On this basis the contribution of the progeny can be written

as $\frac{nxs_1}{2NXS_1} + \frac{n(1-x)s_2}{2N(1-X)S_2}$. The result is that s_1 and s_2 cancel out and what is left yields $\frac{n}{2N}\left(\frac{x}{X} + \frac{1-x}{1-X}\right)$ the same as formula (1). As long as the males and females of the progeny have the same viability as those in the G_1 at large, any difference between the sexes in viability does not enter the picture. Thus, it is the primary sex ratio which concerns us and to which the conclusions already drawn apply.

These conclusions are based on the assumption that the number of zygotes produced by a given parent is independent of the sex ratio in his progeny. Fisher considers a case where this assumption does not hold, the case where parents care for the young. Suppose, for example, that males die more often than females. The male zygotes in any progeny will tend to die off and relieve the parent of the burden of caring for them. The higher the proportion of male zygotes in the progeny to start with, the more zygotes die and the more parental energy is made available for the production of new zygotes. Thus C_m in such cases is increased because n is increased. This will result in the establishment of a primary sex ratio in favor of the males. In the same way wherever parental care occurs the primary sex ratio will be adjusted so that there is an excess of the less viable sex.

DISCUSSION

If we ignore instances involving parental care, intergroup selection and sex-linked genes, the conclusion of the foregoing analysis can be stated as follows: Whenever the primary sex ratio of a population is not 0.5, selection favors sex ratio genes whose increase in frequency will cause a shift closer to 0.5. When the population sex ratio is already 0.5 there is no selection for sex ratio genes no matter what the direction or magnitude of their effects.

This means that the 1:1 sex ratio may result not out of any immutability of this ratio but because selection establishes it as an equilibrium value. A new mutant sex ratio gene occurring in a population which has already attained this equilibrium will shift the sex ratio of the population somewhat and bring about selection against itself.

However, selection against the gene will not always be very stringent. In a large population the gene may be in a very low frequency. The effect on the population sex ratio will then be slight. Selection will be weak, and the gene may persist a good while. Further, it may persist indefinitely even at a high frequency provided its effect is balanced by genes at other loci so that the population sex ratio is 0.5.

If sex ratio genes are actually present in a population two things might be expected. First, selection for high and low sex ratios should be possible; and, second, the frequency of progenies showing extreme sex ratios should be higher than expected on the basis of the frequencies of male and female zygotes in the whole population.

These two expectations are perhaps fulfilled in some observations of long standing which have so far been difficult to interpret. King (1918) in selection experiments on rats obtained high and low lines for sex ratio. Prevosti (1940) confirms the older observations of Geissler, summarized by Stern (1949), to the effect that human families show a higher than expected frequency of extreme sex ratios.

SUMMARY

The population genetics of autosomal genes affecting the primary sex ratio is discussed. It is shown that a gene may be expected to increase in frequency if its increase will shift the sex ratio of the population nearer to 1:1. It is suggested that it should be possible to alter the primary sex ratio by selection.

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ON COADAPTATION IN DROSOPHILA*

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Chromosomal polymorphism within Drosophila species is the basis of much that is known concerning the mode of operation of natural selection in evolution. The existence of geographical gradients in the frequencies of different gene arrangements indicates a differential response of contrasting genotypes to environmental clines; the varying frequencies of inversion types within single populations reflect temporal changes in selective forces; and the simultaneous maintenance of different inversion types within a local population *over a long period* of time attests to the adaptive superiority of structural heterozygotes over structural homozygotes within that population. The varying frequencies of the inversions allow inferences as to their selective responses; their cytological appearance, if they overlap one another, permits a reconstruction of their phylogeny.

The frequency of a given inversion within a population is not governed solely by the interaction of the physiological characteristics of its carriers with the environment. The cytogenetic interrelations of inversion types to one another and the influence of these on gamete formation and fertility are also important. Pericentric inversions serve as an example; crossing over within these inversions results in the formation of aneuploid gametes—gametes carrying duplications and deficiencies. The inviable zygotes produced by such gametes reduce the effective fertility of individuals heterozygous for this type of inversion. One would expect pericentric inversions to be rare in natural populations and, in general, this expectation is fulfilled although exceptions are known (Miller, 1939; Carson and Stalker, 1947). Certain pairs of included or overlapping inversions can also give rise to aneuploidy following recombination. The simultaneous presence of two such inversions in a population exposes both to adverse selection; within any one population one or both of such arrangements should be rare.

Despite the postulated selection against them, pericentric, included, and overlapping inversions are found in populations. It would seem that selective forces are operating that compensate for the deleterious effects of such kinds of inversions in populations. A sufficiently potent selective force is the high adaptive value possessed by some inversion heterozygotes. Dobzhansky (1950) has shown that this superiority is the result of the "coadaptation" of the gene complexes in chromosomes of one arrangement with those of another arrangement within an interbreeding population. It is suggested here that the inversion types co-existent within a population are those that permit coadaptation to occur most readily.

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Wallace and King (1950, 1952) and Wallace et al. (1953) have shown that experimental populations of *D. melanogaster* may differ in adaptive values; that the adaptive value of a population is relatively independent of the frequency of lethals, semilethals, and other major gene mutations in its gene pool; and that the interactions of genes from the same pool differ from those of genes from different pools. Selection for mutually compatible alleles and gene complexes within these populations leads to coadaptation. In a sense, a population possessing two inversion types, *A* and *B*, undergoes coadaptation at two levels: (1) The coadaptation of different chromosomes with the same arrangement leads to the superiority of *A′/A″*, *A′/A‴*, *B′/B″*, heterozygotes, over *A′/A′*, *A″/A″*, *B′/B′*, homozygotes. (2) Coadaptation between the different arrangements leads to even higher adaptive values of *A/B* heterozygotes. The gene pool of a population of this sort is a double one: selection coadapts the two sections of the pool to one another and, simultaneously, produces internal coherence within each section.

The gene content of inverted chromosomal segments are effectively separated because of the reduction in recombination (see Dobzhansky and Epling, 1948, and Carson, 1953, for data on *D. pseudoobscura* and *D. robusta*, respectively). This is true of simple inverted chromosome sections and of segments involving overlapping inversions. There exist, however, series of three inversions, which may be referred to as triads, such that I has given rise to II by a simple inversion and, subsequently, II to III by another, but overlapping, inversion. If all three members of such a triad are present within a single, interbreeding population, the chromosomal segments and their inverted blocks of genes are not genetically separated from one another. The top portion of fig. 1 illustrates such a triad; the order of the letters represents the structural arrangement while the type of print serves to identify the source of the genes found within the different arrangements. Points of breakage are designated by the black triangles. The center portion of the figure shows each of the three possible combinations of the three arrangements and (x—x) the regions of the chromosomes within which recombination cannot occur. The arrangements identified as I′, I‴, II′, etc. at the right of the figure represent chromosomes with given arrangements which have aquired genes from other arrangements outside the limits of the differentiating inversions. If any two of these arrangements were the only two present within a population, the underlined segments would not undergo recombination, the genetic material within these segments would be maintained intact as a unit, and, presumably, these would be the coadapted portions of the chromosomes. On the other hand, if all three arrangements were present in a population, individuals carrying the combinations of chromosomes indicated at the bottom of the figure would be formed. Each of these combinations is structurally homozygous and, hence, crossingover can occur freely throughout the length of the chromosome. It is now obvious that the integrity of the genetic material within the inverted segments is lost and the coadapted combinations are now broken up. For instance, if only arrangements I and II were present within a popu-

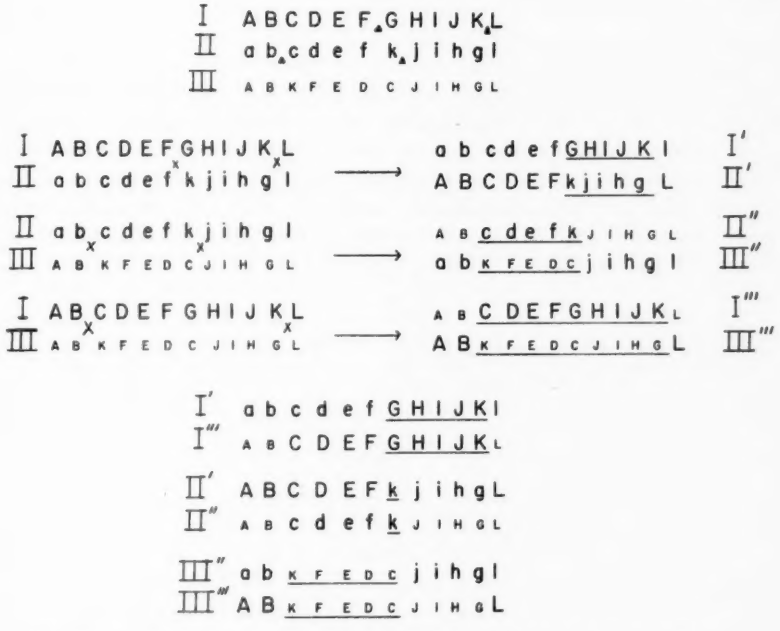

FIGURE 1. Recombination between chromosomes possessing inverted gene sequences. See text for detailed explanation.

lation, the gene-block GHIJK was always contrasted with kjihg. Within a population containing all three inversions, arrangement I maintains its segment GHIJK but arrangement II can acquire any combination of kjihg and kJIHG. The integrity of the coadapted complex has been lost and coadaptation, if not impossible, has been made extremely difficult.

Thus, in addition to the long recognized selection against aneuploidy (see Sturtevant, 1938, and Novitski, 1946) as a determiner of inversion frequencies and distributions, there may also be a selection based on chromosomal mechanisms facilitating coadaptation. It is possible in many instances to infer whether the absence of one inversion from a population that contains another is the result of selection against the formation of aneuploid gametes or against interference with coadaptation. If the basis of selection is aneuploidy, the inversion types which exclude each other must be of the sort that, through crossing over, give rise to duplications and deficiencies. Populations that have high frequencies of one inversion should have low frequencies of the other; this relationship should be independent of other inversions that may also exist within the population. If, however, selection stems from the interference of triads with coadaptation, the cause lies in the simultaneous presence of all members of the triad, i.e., of three serially related inversions. No single population should possess high frequencies of all three members of a triad; at least one of the three should be rare. Data bearing on these alternative hypotheses

taken from Dobzhansky and Epling (1944), Carson and Stalker (1947), and Levitan (1951) are presented in tables 1, 2, and 3.

In table 1 are listed pairs of chromosomal inversions that, theoretically, can give rise to duplications and deficiencies among crossover products. Selection, consequently, might oppose the simultaneous presence of high frequencies of both members of each pair in the same population. Among the data listed there are numerous exceptions to this expectation: In *D. robusta* XR1 and XR2 are present together in high frequencies in three populations, 2L1 and 2L2 in two populations, and 2L1 and 2L3 in one or two; in *D. pseudoobscura* AR and PP as well as ST and SC are found to-

TABLE 1

PAIRS OF CHROMOSOMAL ARRANGEMENTS WITHIN *D. robusta* AND *D. pseudoobscura* WHICH ARE CAPABLE OF PRODUCING ANEUPLOIDY BY CROSSING OVER. SELECTION SHOULD PREVENT SIMULTANEOUS HIGH FREQUENCIES OF BOTH MEMBERS OF EACH PAIR WITHIN ANY ONE POPULATION. THE OBSERVED PERCENTAGE FREQUENCIES OF THE INVERSION TYPES ARE LISTED TO THE RIGHT OF THE PAIR. DATA THAT SEEMINGLY DISAGREE WITH THE HYPOTHESIS ARE ITALICIZED. THE PERCENTAGES NEED NOT TOTAL 100% BECAUSE OF OTHER ARRANGEMENTS WITH THE POPULATION.

Species	Inversion pair	Observed frequency in different localities
*D. robusta**	XR1-XR2	93-2, 35-*23*, 61-1, 53-*29*, *29-54*, 0-96, 0-12
	2L1-2L2	9-4, 3-6, 41-8, 15-3, *44-24*, *73-14*, 28-5
	2L1-2L3	9-31, 3-11, 41-1, 15-0, 44-0, 73-0, *28-25*
	2L2-2L3	4-31, 6-11, 8-1, 3-0, 24-0, 14-0, 5-25
*D. pseudoobscura***	CH-TL	10-3, 10-5, 14-4, 5-8, 9-7, 15-6, 8-2, 29-4, 11-0, 15-1, 2-0, 7-0, 0-2, 4-1, 3-3, 0-2, 0-6, 0-12, 0-17, 61-1
	AR-PP	47-3, 30-2, 54-2, 34-1, 48-0, 20-0, 14-0, 26-0, 26-0, 56-0, 96-1, 87-2, *63-26*, *78-18*, *27-66*, *26-71*, *21-70*, *12-70*, 3-72, 7-27
	ST-SC	37-0, 53-0, 24-1, 38-1, *28-12*, *49-10*, *46-31*, 42-0, 58-5, 27-0, 2-0, 4-0, 3-0, 1-0, 0-2
	TL-CU	*25-50*, *17-36*, 24-9

* Except for the last percentage-pair of each Inversion pair which is from Levitan (1951), the data for *D. robusta* are from Carson and Stalker (1947).

** Data for *D. pseudoobscura* are from Dobzhansky and Epling (1944).

gether in many populations. CH and TL in *D. pseudoobscura* and 2L2-2L3 in *D. robusta* seemingly offer no exceptions.

Table 2 presents the frequencies of individual members of various inversion triads whose simultaneous presence within a locality could disrupt selection for coadapted genetic systems. In the triad XL-XL1-XL2 of *D. robusta* there is one instance in which all three inversions are found in relative abundance (76%-15%-9%, respectively); otherwise the frequencies of these three inversions fit the requirements of the hypothesis by having at least one arrangement rare in each locality. In the 2L-2L2-2L3 triad at least one inversion is rare in each collection. The 2L-2L1-2L3 triad presents the most marked exception to the "coadaptation" hypothesis; Levitan

TABLE 2

CHROMOSOME INVERSIONS CAPABLE OF TRANSFERRING GENES SERIALLY FROM ONE TO THE OTHER BY CROSSING OVER—TRIADS, IN THE TERMINOLOGY OF THE TEXT. IF THIS TRANSFER DISRUPTS COADAPTATION AND IF COADAPTATION IS AN IMPORTANT PHENOMENON, POPULATIONS SHOULD NOT POSSESS ALL THREE MEMBERS OF ANY ONE TRIAD SIMULTANEOUSLY. THE OBSERVED FREQUENCIES OF THE MEMBERS OF EACH TRIAD IN DIFFERENT LOCALITIES ARE LISTED AT THE RIGHT; DATA THAT SEEMINGLY DISAGREE WITH THE "COADAPTATION" HYPOTHESIS ARE ITALICIZED. PERCENTAGES NEED NOT TOTAL 100% IN EACH LOCALITY BECAUSE OF OTHER INVERSIONS.

Species	Inversion triad	Observed frequencies in different localities (%)
*D. robusta**	XL-XL1-XL2	52-48-0, 41-58-1, 98-1-1, 76-15-9, 64-0-36, 81-0-19, 40-59-1
	2L-2L2-2L3	56-4-31, 80-6-11, 50-8-1, 82-3-0, 31-24-0, 13-14-0, 42-5-25
	2L-2L1-2L3	56-9-31, 80-3-11, 50-41-1, 82-15-0, 32-44-0, 13-73-0, *42-28-25*
*D. pseudoobscura***	CH-SC-TL	9-12-7, 15-6-10, 8-2-40, 11-5-0
	AR-PP-ST	47-3-37, 30-2-53, 54-2-24, 34-1-38, 48-0-28, 20-0-50, 14-0-46, 26-0-42, 26-0-58, 56-0-27, 96-1-2, 87-2-4, 63-26-3, 78-18-0, 27-66-1, 26-71-0, 21-70-0, 12-70-0, 3-72-0, 7-27-0
	TL-SC-CU	25-0-50, *17-38-36*, 24-65-9

* See footnote, table 1.
** See footnote, table 1.

(1951) reports frequencies of these three inversions at Englewood Cliffs, New Jersey, as 42%-28%-25%. In *D. pseudoobscura* the AR-ST-PP triad demonstrates very strikingly the situation expected on the coadaptation hypothesis: In the data recorded on the first ten localities, PP is a rare chromosome whose frequency never exceeds 3%; in six other localities PP is one of the common chromosomes and, simultaneously, ST becomes exceedingly rare. Within the TL-SC-CU triad, two localities agree with the expectation in having 2 common arrangements and one rare one; one locality is exceptional in having all three present. This last locality will be examined in more detail below.

Finally, table 3 presents data on sets of three chromosomal inversions that, since they are not members of a triad, should not interfere with coadaptation within an interbreeding population. In the case of XR-XR1-XR2 of *D. robusta* there are three localities recorded in which all three inversions are present with high frequencies. In two populations of the same species 2L-2L1-2L2 also occur together. In *D. pseudoobscura* AR-ST-CH and AR-ST-SC frequently comprise the bulk of the third chromosomes of local populations with each of the three being very common.

With the notable exception of the Englewood Cliffs population of *D. robusta*, the data on the distribution of inversion types in different popula-

tions of the two species considered here tend to support the coadaptation hypothesis. The data fail, however, to lend complete support to this hypothesis by not demonstrating that each of the three possible pairs of the chromosomes of a triad—i.e., I-II, I-III, and II-III—can co-exist in the absence of the third member. In every instance illustrated, populations consisting of one of the three possible pairs are not found. No known populations of *D. robusta* have simultaneous high frequencies of XL1-XL2, 2L2-2L3, or, with the exception of the Englewood Cliffs population, of 2L1-2L3; no populations of *D. pseudoobscura* recorded in table 2 have high frequencies of ST-PP or of SC-CU. It would be meaningless, of course, to cite the patterns of association shown in table 2 as evidence favoring the second hypothesis if one of the three possible pairs cannot co-exist be-

TABLE 3

SETS OF THREE CHROMOSOME INVERSIONS—NOT TRIADS—WHOSE SIMULTANEOUS PRESENCE WITHIN LOCAL POPULATIONS SHOULD NOT BE SELECTED AGAINST UNDER THE "COADAPTATION" HYPOTHESIS. NO EFFORT HAS BEEN MADE TO GATHER ALL OF THE RECORDED DATA CONCERNING SUCH INVERSIONS; SOME REPRESENTATIVE FIGURES ARE GIVEN FOR COMPARISON WITH THOSE OF THE PREVIOUS TABLE. NOTE ESPECIALLY THE ITALICIZED FIGURES. THE PERCENTAGES NEED NOT TOTAL 100% BECAUSE OF OTHER ARRANGEMENTS.

Species	Inversion types	Observed frequencies in different localities (%)
*D. robusta**	XR-XR1-XR2	5-93-2, *42-35-23*, 38-61-1, *18-53-29*, *17-29-54*, 4-0-96
	2L-2L1-2L2	56-9-4, 80-3-6, 50-41-8, 82-15-3, *32-44-24*, *13-73-14*
*D. pseudoobscura***	AR-ST-CH	47-10-37, 30-10-53, *54-14-24*, 34-5-38, 48-9-28, *20-15-49*, *26-29-42*, *26-11-58*, *56-15-27*
	AR-ST-SC	*48-28-12*, 20-49-10, *14-46-31*
	CU-TL-EP	*50-25-15*

* See footnote, table 1.
** See footnote, table 1.

cause of aneuploidy. However, the absence of populations containing high frequencies of both ST and PP or SC and CU cannot be explained by the aneuploid hypothesis for these pairs of arrangements differ by single inversions. A more detailed examination of some of the data appears to be justified.

The frequencies of the three members of the TL-SC-CU triad of *D. pseudoobscura* listed in our table 2 are consolidated from table 2 of Dobzhansky and Epling (1944). As indicated above, these data fail to support the coadaptation hypothesis in one instance where all the arrangements co-exist with high frequencies. The data as listed indicate, too, that the populations conforming to the hypothesis possess only TL and SC or TL and CU. Casual observation of the detailed and, unfortunately, limited data given

by Dobzhansky and Epling reveals, however, that the actual distribution of chromosome types within smaller localities is not as simple as this consolidation indicates. Figure 2 shows the chromosomes observed in collections extending over a 250–300 mile transect near Mexico City. In this figure large letters represent frequencies over 30%, medium sized letters represent frequencies over 20%, and small letters represent frequencies greater than 10%. Frequencies less than 10% are not shown. The figure demonstrates that different populations do, as a rule, possess only two of these three inversion types and that among these local populations all three pairs of chromosomes of this triad—TL-SC, TL-CU, and SC-CU—are represented. The EP and OL arrangements that are also found in certain

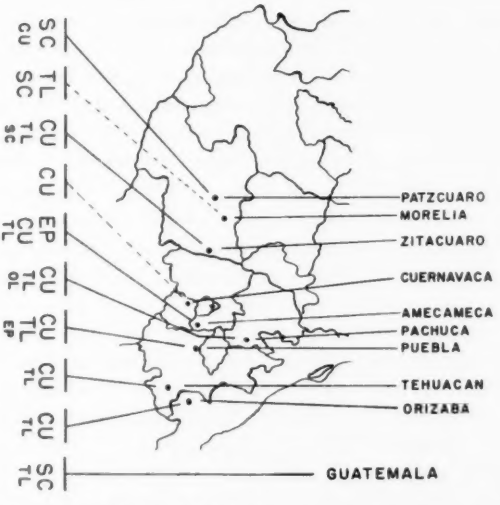

FIGURE 2. The frequencies of third chromosome arrangements of *D. pseudoobscura* in populations near Mexico City. The three sizes of print represent frequencies greater than 10%, 20%, and 30% in that order; frequencies less than 10% are not shown. All of the samples on which this figure is based are small; two extremely small ones are represented by dotted lines. (Data from Dobzhansky and Epling, 1944. Table 2.)

localities do not form triads with the other arrangements in the same localities; these associations compare with those of table 3. Finding all three possible paired combinations of these three arrangements in different populations and, simultaneously, demonstrating that the exceptional distribution of their frequencies indicated in table 2 is not valid lend additional support to the coadaptation hypothesis. The ability to initiate and to maintain coadapted systems, then, must be an important factor in the action of selection within a Drosophila population. Combinations of inverted gene sequences that allow the disruption of selected gene combinations by serial crossing-over from one inversion type to another do not, as a rule, co-exist within the same locality.

The conclusion that the data, as a whole, support the second hypothesis, does not imply that the formation of aneuploid gametes and the resultant partial sterility of certain individuals is unimportant in population genetics. The number of naturally occurring pericentric inversions within Drosophila species is small compared to the number of paracentric ones. (The relative importance of aneuploidy, of course, must be greater immediately after an inversion arises than after coadaptation has become established; one of the few pericentric inversions known—2L3 of *D. robusta*—is extremely common in some populations.) Translocations are even rarer than pericentric inversions (Dobzhansky and Dreyfus, 1943, report a single translocation in a collection of *D. ananassae*); this is undoubtedly the result of the semisterility of translocation heterozygotes. The combinations of inversions listed in table 1 are those that can, by single crossovers, give rise to duplications and deficiencies. This does not mean that they must nor that they do; chiasmata may not form within the region that leads to aneuploidy. It is even conceivable that natural selection within a Drosophila population can lead to a partial localization of chiasmata. On the other hand, the exceptional data of Levitan do not invalidate the basis of the coadaptation hypothesis. First, one of the inversion types in this particular population is a pericentric inversion; this fact may already indicate the existence of modified crossover patterns for this arrangement. Second, within triads of overlapping inversions there are chromosomal segments that are effectively separated and within which coadapted gene complexes can develop; the nature of these separated segments depends upon the amount of overlap, the position of the inversions along the chromosome, and on heterozygosity for inversions in other chromosomes. Third, it is known that some populations of *D. pseudoobscura* possess only a single arrangement of the third chromosome; the ability of a population to adapt to its environment is not wholly dependent upon inversion heterozygosity.

The evidence that interference with coadaptation is a factor of considerable importance in the establishment of inversion types within populations of Drosophila is incompatible with the notion that the adaptive values of inversion types are determined by the breakage points and the inversion patterns themselves. As in the aneuploid hypothesis, preadaptation of inversion types through position effects involves *pairs* of arrangements and is independent of other inversion types in the population. In general, within diploid organisms such as Drosophila, no developmental, meiotic, or other intra-individual phenomenon can govern the distribution of chromosomal arrangements so that only two of three are found within a population. This type of distribution can be governed only by chromosomal interactions at the level of the population gene pool and thus serves to identify the gene pool as the unit of evolution.

There are two explanations to account for the absence from populations of one of the three possible pairs of chromosomes that are members of one triad. One explanation is based on coadaptation; long single inversions do not isolate blocks of genes since double crossovers can exchange seg-

ments within the inverted region. No population of *D. pseudoobscura* possesses ST and PP with simultaneous high frequency and very few populations possess SC and CU. These two inversion pairs are the longest single ones found within this species—both involve more than 50% of the chromosome. The only coadapted complexes that involve more of the chromosome than this are complex ones—60% for AR-PP, 82% for OL-CU, and 56% for ST-CH. The other explanation is based on the fact that any inversion has a definite time and place of origin. Some triads consist of inversions that have never had an opportunity to co-exist in the same locality because of widely separated points of origin; these cases help neither to prove nor disprove the current hypothesis. Other triads consist of inversions, however, that arose in geographically isolated areas (I-II in one area and II-III in another) but, despite the opportunity, have failed to form populations that consist of the third pair (I-III). Direct proof of the occurrence of this opportunity does not exist but, judging from the data of table 3 and figure 2, three arrangements that do not complete a triad are frequently incorporated into the same population; it would be strange if chromosomes that do comprise triads never encounter this opportunity as well.

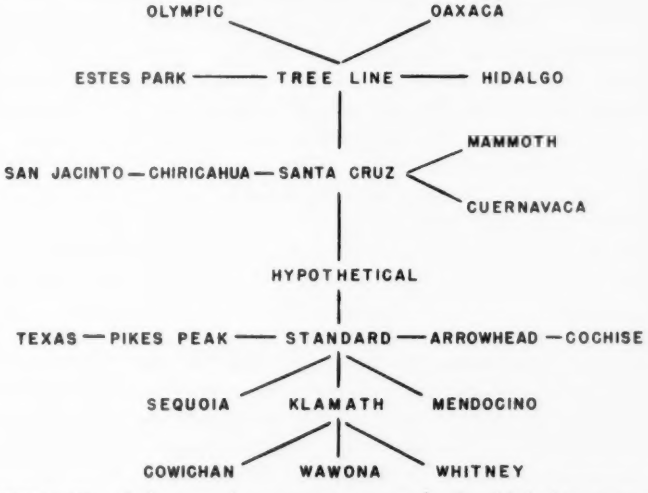

FIGURE 3. The phylogeny of gene arrangements in the third chromosome of *D. pseudoobscura* and *D. persimilis*. The standard arrangement occurs in both species, the lower six shown on the diagram occur only within *D. persimilis*, and the remaining ones occur only within *D. pseudoobscura*.

Within the phylogeny of inversion types of *D. pseudoobscura* constructed by Dobzhansky (fig. 3), one of the most interesting arrangements is "Hypothetical" (HY). At one time there were two hypothetical arrangements; one of these (SC) was subsequently identified in a collection from Santa Cruz Island, California. The remaining hypothetical arrangement has not been found and as more and more data accumulate it becomes increasingly

improbable that it exists in nature. The position of HY on the phylogenetic tree is important in connection with the coadaptation hypothesis. One of the three inversions of any triad is generally rare within any one locality; HY participates in six triads: (1) HY-ST-PP, (2) HY-ST-AR, (3) HY-SC-CH, (4) HY-SC-TL, (5) ST-HY-SC, and (6) HY-SC-CU. It is tempting to ascribe the absence of HY from present populations to selective forces involved in the formation of coadapted systems; simultaneous opposition by selection within several triads may have been instrumental in HY's extinction.

Epling (Dobzhansky and Epling, 1944) has presented a hypothesis to account for the observed distribution of inversion types within the species range of *D. pseudoobscura*. This hypothesis antedated the demonstration of large selective differentials between individuals of contrasting genotypes and, consequently, a disproportionate emphasis was placed upon the distribution of inversions from points of origin by a process of slow diffusion. Epling concluded that the inversion types and, consequently, the species, must have existed during the Miocene or even before. Mayr (1945) disputed Epling's hypothesis of ancient origin by suggesting that the inversion types possess definite selective values. On Mayr's hypothesis the gene content of chromosomes of the same arrangement may vary considerably from locality to locality and the entire distribution of inversions throughout the species range could have occurred within a very short time—since the Pleistocene, for instance. The phenomenon of coadaptation and the distribution of inversion types in a manner compatible with the formation of coadapted complexes allow further refinements of Mayr's concept. In the development of coadaptation by selection, combinations of inversions seem to serve simply as mechanisms that retain blocks of genes intact. Just which genes are accumulated and retained within each inversion of a combination seems to be decided within the local populations (Dobzhansky, 1950). The mechanisms of gene separation afforded by inversions are such that they break down if all three members of a triad co-exist in the same population. Consequently, the distribution of inversion types within *D. pseudoobscura* can be examined in the light of "coadaptation mechanisms" or "inversion complexes" rather than in terms of the individual inversions: What inversion types comprise the bulk of various populations throughout the species range? The distribution of these major complexes has been charted in figure 4. Since the emphasis is on major systems of coadaptation, inversion frequencies less than 10% have been ignored. It can be seen from the figure that within the United States (and most of the data come from this country) there are three major inversion complexes utilized in the development of local coadaptation: In the far west from Canada to Mexico there is an ST-AR complex that may or may not involve CH; along the Pacific coast in south and central California there is a new association of ST-AR with SC; and in the southwest (Texas, Colorado, and New Mexico) there is a AR-PP inversion complex. A broad zone of AR (some populations in this zone approach 100% AR) separates the ST-AR and the AR-PP complexes—a separation that, in part, gave rise to the data supporting the

FIGURE 4. The main associations of third chromosome arrangements within the continental United States and neighboring localities. The three sizes of print designate frequencies as described in Fig. 2.

triad hypothesis. Farther south, in Mexico and Guatemala, the mechanisms of coadaptation change; some of these latter mechanisms are shown in figure 2. (See, too, Dobzhansky, 1948.)

The inversion phylogeny of *D. pseudoobscura* is intimately related to that of its sibling species *D. persimilis* and, to a lesser extent, to that of *D. miranda*. These latter species occupy much smaller ranges than *D. pseudoobscura*; one might describe these ranges merely as Washington, Oregon, and the northern two-thirds of California. Sturtevant (1938) suggested that the separation of *D. persimilis* from *D. pseudoobscura* (known then as races B and A of *D. pseudoobscura*, respectively) resulted from the co-existence of AR and KL (Klamath) arrangements of the third chromosome in the same

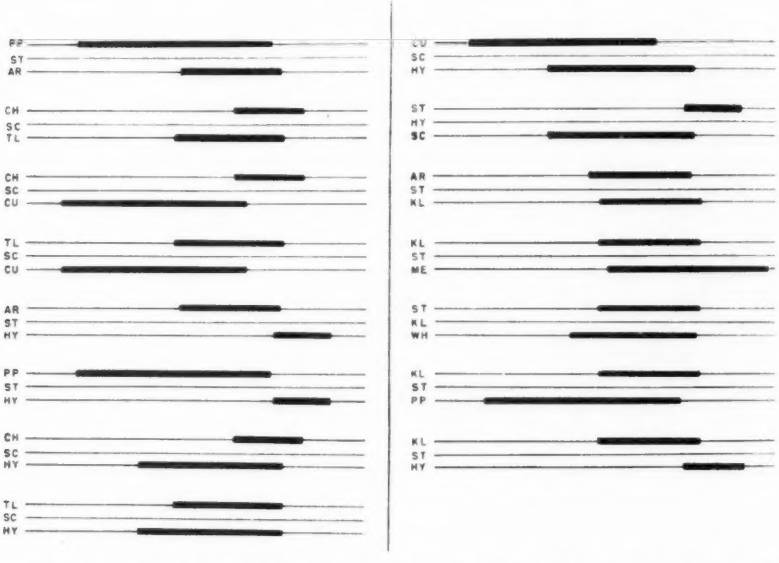

FIGURE 5. The relative sizes and positions of the inversions of different triads in *D. pseudoobscura* and *D. persimilis*. The center arrangement of each triad is regarded as uninverted.

geographic area. This hypothesis was based on the overlap of these two inversions and the production of aneuploid gametes by crossing over. It seems hardly likely that this hypothesis is correct because, as can be seen from figure 5, the AR-PP complex that exists over most of the southwest has as much overlap as the AR-KL complex and seemingly offers as great a chance for aneuploid formation. Furthermore, the two major complexes found within *D. persimilis* at the present time are KL-ME and ST-WH; each of these complexes is characterized by an overlap as great as or greater than that found in AR-KL.

An alternative hypothesis to explain the origin of *D. persimilis* can be based upon triads, the maintenance of coadapted systems, and the distribu-

tion of the two major inversion complexes found in California. Suppose that two inversion mechanisms for establishing coadaptation—SC-HY and ST-AR —existed in well defined, geographically separated areas of the United States and Mexico much as the ST-AR and AR-PP complexes exist in different regions of the United States today. Suppose, further, that these were efficient mechanisms, that they extended their ranges (not in the sense of a migration of given chromosomes but by the adoption of the one mechanism or the other by local populations near the established distribution areas), and that finally their ranges met in California. The introduction of the sequence SC-HY-ST-AR into interbreeding populations along the zone of contact would lead to a disruption and general breakdown of both coadapted systems within this region. Judging from Vetukhiv's results (1953) and from unpublished data of Brncic, a reduction of adaptive value from this sort of phenomenon can be substantial. Local semi-isolated populations in which genetic systems with relatively high adaptive values were established could have developed within this zone of generally lowered adaptive values (see Dobzhansky and Pavlovsky, 1953). If its adaptive value were sufficiently higher than those of surrounding populations, a locally coadapted system could have been maintained despite substantial contact with migrants from other populations. Constant exposure to this migration and the preservation of the locally established complex by selection in spite of this contact would lead eventually and automatically to sexual isolation if the requisite genetic variability were present; "automatically" because those surviving individuals possessing the coadapted complex each generation would be the product of intra-population matings (see Koopman, 1950).

Three situations can be regarded as derivatives of this contact between two large populations bearing incompatible adaptive mechanisms: (1) The ST-AR-SC complex of the west coast represents a relic of the former SC-HY complex. SC, after HY was eliminated from these populations, no longer formed a triad with ST-AR and became incorporated into the coadapted complex of the California population. (2) The species distribution of *D. persimilis* coincides with the area of overlap of the ST-AR-(CH) and ST-AR-SC complexes. (3) The current inversion phylogeny (third chromosome) of *D. persimilis* stems from ST.

The above account, admittedly speculative, does not bear upon the Epling-Mayr discussion of the age of either inversions or species. In that the present hypothesis gives an active role to selection for various inversion types, it concurs with Mayr's assumption that changes in inversion distributions could have occurred within *D. pseudoobscura* at a relatively rapid pace. It adds to the former discussions the concept that it is not only possible for inversion types to predate species formation but that, with the system of coadaptation utilized in these species, it is necessary that some of these do so.

A great deal of emphasis has been placed here upon *D. pseudoobscura* and *D. persimilis*. This is only natural for it is within these species (and

D. robusta) that frequency data are available for the distribution of chromosomal inversion types. However, examination of data of *D. prosaltans* (Cavalcanti, 1948), *D. azteca* (Dobzhansky and Sokolov, 1939), *D. athabasca* (Novitski, 1946), *D. nebulosa* (Pavan, 1946), and *D. ananassae* (Kikkawa, 1938) failed to reveal any situation opposed to the triad hypothesis. For instance, Novitski presents a phylogeny that consists of 19 triads; many of the arrangements are hypothetical since the original material examined was small. Of the 19 triads, one is composed entirely of hypothetical arrangements, 8 contain two hypotheticals and one observed arrangement, 9 contain one hypothetical and two observed, and only one has all three arrangements actually observed. Within the localities from which Novitski obtained his material, then, we can conclude that most had high frequencies of no more than two members of a given triad. Within the B chromosome of *D. azteca* there are seemingly two Mexican complexes—an alpha-beta and a beta-gamma complex. Collections are not sufficiently large to reveal if the two complexes meet throughout an extensive area.

It seems likely that *D. melanogaster* and *D. funebris* do not utilize inversions to the extent that some of the other Drosophila species do. Dubinin, Sokolov, and Tiniakov (1937) report on extensive observations of these two species with only the most meager frequencies of inversions present. On the other hand, *D. willistoni* seemingly utilizes inversions in a different manner. Whereas *D. pseudoobscura* and *D. persimilis* possess few large inversions on a single chromosome, *D. willistoni* possesses numerous small inversions scattered throughout the length of all chromosomes; as many as 16 inversions have been observed in the heterozygous condition within a single individual of this species. The number of inversions here is so great and so little is known in the way of precise patterns of distribution and association that little can be said other than that these mechanisms for coadaptation appear to differ at least somewhat from those of the temperate regions.

Many of the consequences of the coadaptation hypothesis are subject to experimental verification. Dobzhansky and Pavlovsky (1953) have reported on the origin of coadaptation within experimental populations; triads should be incapable of participating in this "mesoevolution." It has been suggested that double crossovers between ST and PP and between SC and CU prevent the formation of stablized coadapted systems; these pairs of chromosomes, then, should not give rise to new stable coadapted systems of the type described by Dobzhansky and Pavlovsky. Finally, the hypothesis indicates that natural populations within which all three members of a triad co-exist in high frequency are exceptional ones; coadaptation and the superiority of heterozygotes should be upset in these populations if the members of the triads co-exist because of recent distributional changes.

SUMMARY

The coadaptation of the gene complexes carried by different gene arrangements within a population depends upon the integrity of the genic

contents of the inverted segments. Certain combinations of inversions—triads, in the above account—destroy this integrity by facilitating serial transfer of genes from one arrangement to another by crossing-over. Since the different inversions of a population are generally coadapted, populations should possess with high frequency, at most, two of the three inversions of any one triad. In general, the data from populations of *D. robusta* and *D. pseudoobscura* support this hypothesis; one member of each triad is usually absent or rare within any one locality. Three inversions that are not members of a triad should not be opposed by selection and, in agreement with the hypothesis, three such inversions are frequently present in populations with high frequency. We conclude that coadaptation frequently outweighs aneuploidy as a selective force in determining inversion frequencies within populations. The possible role of triads in the geographical distribution of inversions and in speciation are also discussed.

ACKNOWLEDGMENTS

The author wishes to express his appreciation for the many interesting and profitable discussions of these problems he has had with Professor Th. Dobzhansky, Columbia University, and Dr. J. C. King, The Biological Laboratory.

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NOVEL VARIATION IN TOMATO SPECIES HYBRIDS*

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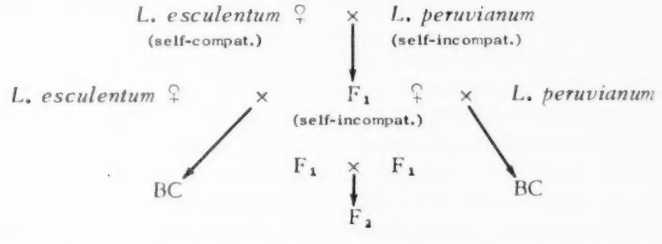
In the breeding of improved forms of the cultivated tomato, *Lycopersicon esculentum*, more and more attention has been paid in recent years to its hybrids with the green-fruited species—members of the subgenus Eriopersicon (Muller, 1940). The species *L. peruvianum*, for example, has been particularly useful because it possesses resistance to spotted wilt, curly top, verticillium wilt, root-knot nematode, and other pests, and also because its fruits have a very high content of vitamin C.

Aside from these traits *L. peruvianum* is relatively worthless as a horticultural plant. Like other members of its subgenus, its fruits are small, cherry-size, and retain a greenish color at maturity. The fruits, moreover, have a flavor that is not agreeable to most observers, and they tend to bruise and split easily on handling. The main objective in breeding programs utilizing these species, therefore, is to inject from them into *L. esculentum* one or a few desired traits with the least possible transfer of the objectionable characters.

Hybridization programs with these objectives have encountered a number of difficult obstacles. The F_1 hybrids are difficult to obtain in the first place. Most of the hybrids have been secured by means of embryo culture, the method having first been utilized by Smith (1944). Even when the hybrid is obtained, it yields an F_2 only with great difficulty if it is selfed. This obstacle, construed at first entirely as hybrid sterility, can now be partly circumvented by intercrossing two F_1 plants, thanks to McGuire's (1950) discovery that the F_1 is as completely self-incompatible as the *peruvianum* parent. Furthermore, backcrosses between certain hybrids and *L. esculentum* are almost as difficult to obtain as the original hybrids themselves.

An outline of the compatibility relations of the *esculentum-peruvianum* hybrids is essential to an understanding of the present investigation. McGuire (1950) reported the following successful mating combinations. In spite of many attempts, all other combinations failed to set fruit.



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In short, the only combinations that yield progeny are those in which *L. esculentum* or its derivatives are used as female parents.

The cytogenetic relationships of this species hybrid, in addition to their theoretical interest, have an important bearing on its use for breeding purposes. A project has therefore been undertaken to study the nature of inheritance and to survey the parental forms and their compatibility relations. No attempt is made here to cover all these aspects; instead, the purpose of this report is to call attention to unusual variants that have been encountered in the course of studying the hybrid progenies.

MATERIALS

The first variants were encountered in the F_2 of the original F_1 obtained by Smith (1944) between *L. esculentum* var. Michigan State Forcing and *L. peruvianum* var. *dentatum* PI 128,657. For sake of convenience this hybrid will be designated hereafter as Hybrid No. 1.

When Hybrid No. 1 was first obtained its unfruitfulness was thoroughly appreciated but its compatibility relations were not understood. In the hope of overcoming the barrier of unfruitfulness by dint of large numbers, 15 plants of this hybrid, propagated clonally, were placed in an isolated plot with very wide spacing between plants. As a result of very favorable growing conditions, the clone produced well over 100,000 flowers, which yielded about 350 fruits. The total seed yield was about 150, of which 70 germinated. Forty-six plants were retained and grown to maturity. This reproductive rate is 0.007 offspring per flower in contrast to the 50–100 normally obtaining in either parent species.

Hybrid No. 2, for the use of which the writers are indebted to Dr. J. W. Lesley, was obtained by him (reported by Dr. Margaret M. Lesley, 1950) between *L. esculentum* var. Pearson and *L. peruvianum* PI 126,946. Like No. 1, this hybrid also proved to have a very high level of self-incompatibility, but, when hybridized with No. 1, nearly all pollinated flowers set fruit. The mean number of seeds per fruit was 5–15, a much lower level of fertility than that of the parents, but at least 10,000 times as fertile as Hybrid No. 1 selfed (McGuire, 1950).

A group of six F_1 hybrids that were obtained between several lines of *L. esculentum* and a wild tomato that agrees with Muller's (1940) description of *L. peruvianum* var. *dentatum* are collectively designated Hybrid No. 3. The wild parent had been collected near Tacna, Perú as No. 30349 by the Third Expedition to the Andes by the University of California Botanical Garden. Lamm (1953) and Rick (1953) have shown that, in view of the recently discovered facts that this entity is readily distinguished morphologically and is separated by strong compatibility barriers from the remainder of the *peruvianum* complex, it should be recognized as the separate species, *L. chilense*, which has been described by Dunal in De Candolle's Prodromus (1852). Hybrids with *L. esculentum* are somewhat easier to obtain with some forms of this species than with representatives of typical *L. peruvianum* or *L. peruvianum* var. *dentatum*, although they still seem to require embryo culture for survival.

Of the six hybrids of group No. 3, three belong to one incompatibility genotype, the other three to the other, behaving in agreement with McGuire's (1950) proposals. It has not been possible to hybridize plants belonging to the same incompatibility genotype, but abundant seeds are produced after crossing plants belonging to different genotypes.

VARIANTS IN THE PROGENY OF HYBRID NO. 1

The first two variants to be described appeared in an F_2 of 46 plants that was derived from the selfing of Hybrid No. 1 as indicated above. Although F_2 generations of this species hybrid segregate for a great many character differences with such a wide array of recombinations of parental characters that no two individuals ever seem alike, the form of these variants lies entirely outside the normal range of segregation.

FIGURE 1. Representative leaves of variant and parental species. From left to right: *L. esculentum,* Michigan State Forcing; *L. peruvianum* var. *dentatum* PI 128,657; three leaves of the F_2 variant, 46L241-37. Lower right: typical inflorescence of the variant. Scale at left in cm.

46L241-37 *Entire leaf.* A single plant was encountered in the F_2 having extreme reduction in the number of leaf segments. The blade of many leaves was represented by a single unbroken lamina; in others a few small lateral segments appeared near the base of the abnormally long terminal segment. The leaves were noticeably darker green than those of the normal type and were somewhat rugose. Other features accompanying the leaf modification were reduction in vigor of the plant and slight asymmetry of the flower. In figure 1 the leaves of this variant are compared with those of the parental species.

The size of the terminal leaf segment varies considerably in different accessions of *L. peruvianum,* but in many hundreds of plants of this species, including PI 128,657, grown at Davis under similar conditions, no leaves so extremely reduced as those of this variant have ever been seen. In *L. esculentum* each of the two recessive genes *c* ("potato leaf" described by Price and Drinkard, 1908) and *e* (or *b,* "entire leaf" described by Butler, 1951) effectively reduces the number of leaf segments and also produces a rugose surface, but neither reduces the number of lateral segments so completely or has corresponding effects on vigor and floral morphology. In combination *c* and *e* may condition leaves that are entire and also distorted along the midrib as in the variant, but different in other respects. Furthermore, neither of these genes was present in the pedigree of the *esculentum* parent.

FIGURE 2. Representative inflorescences of variant and parental species. From left to right: *L. esculentum* var. Michigan State Forcing; *L. peruvianum* var. *dentatum* PI 128,657; F_2 variant 46L241-33. Scale at left in cm.

46L241-33 *Compound inflorescence.* In this variant inflorescences are so greatly subdivided that each one bears several hundred flowers. Although inflorescences of the *esculentum* parent seldom branch and those of *L. peruvianum* branch only once or twice, those of the variant undergo six or seven cycles of branching during development, each cycle being referred to hereafter as an order of branching. In respect to number of flowers per cluster, the *esculentum* parent may produce 3 to 9, *L. peruvianum,* 15 to 40, the F_1 hybrid, 8 to 20, and the mutant, 200 or more. Typical inflorescences of this variant and parents are illustrated in figure 2.

No proliferations of this sort have ever been seen in any of our cultures of *L. peruvianum;* branching of the third, but no higher, order is seen in occasional specimens in certain accessions. A gene *s* ("compound inflorescence" described by Crane, 1915) produces somewhat similar effects in *L. esculentum,* but branching is usually limited to the fourth or fifth order and it is certain that this gene was not present in the parent belonging to that species.

ORIGIN OF THE VARIANTS FROM HYBRID NO. 1

At this point attention should be called to several additional facts that were ascertained in this study. In the first place these freaks have appeared only in the progeny of Hybrid No. 1 selfed and of crosses between members of Hybrid No. 3, but none have appeared in F_2 progenies derived by crossing F_1 plants belonging to any two different groups. Thus in 208 seedlings from the cross of Hybrid No. 1 and No. 2 no variants appeared that were similar or comparable to the two already described. Likewise, no exceptional plants were encountered in an F_2 of 69 plants derived from crossing hybrids of groups 2 and 3.

In the second place, additional information was obtained concerning the inheritance of the variants. Opportunities for testing the genetic nature of these conditions was limited to crosses with *L. peruvianum.* Crosses with *L. esculentum* proved almost as difficult as the initial one between the two species, and the diseased condition and incompatibility relations interfered with crosses with the F_1 hybrid.

Hybridization of each of the two variants with *L. peruvianum* yielded progeny exclusively of normal phenotype.

Second-generation populations of the entire-leaf variant were then produced by mating pairs of F_1 hybrids of the same parentage. In a total of 116 F_2 plants four were sharply distinguished from the rest by the near absence of lateral leaf segments. Among the remainder of the population the proportional length of the terminal segment varied considerably showing that the responsible genes are not completely recessive in their action. Representative leaves from a sample of the population are shown in figure 3.

Segregating progenies were not obtained for compound inflorescence.

The data are obviously too limited to permit an extensive genetic analysis. Furthermore, the extremely heterozygous nature of the *peruvianum* parent, particularly the known variation in length of terminal segment, would render such an analysis even less trustworthy. At least it can be said that each character behaves as if partly or completely recessive, and that, for entire leaf, apparently two or three genes interact to effect the mutant phenotype.

The following sources of novel variation in species hybrids are considered in respect to the facts known about these two variants.

1. *Mutation.* Sturtevant (1939) suggested that the high rate of mutation he observed in hybrids of races A and B of *Drosophila pseudoobscura* might have been provoked by the hybrid condition *per se.* Likewise, Baur (1932)

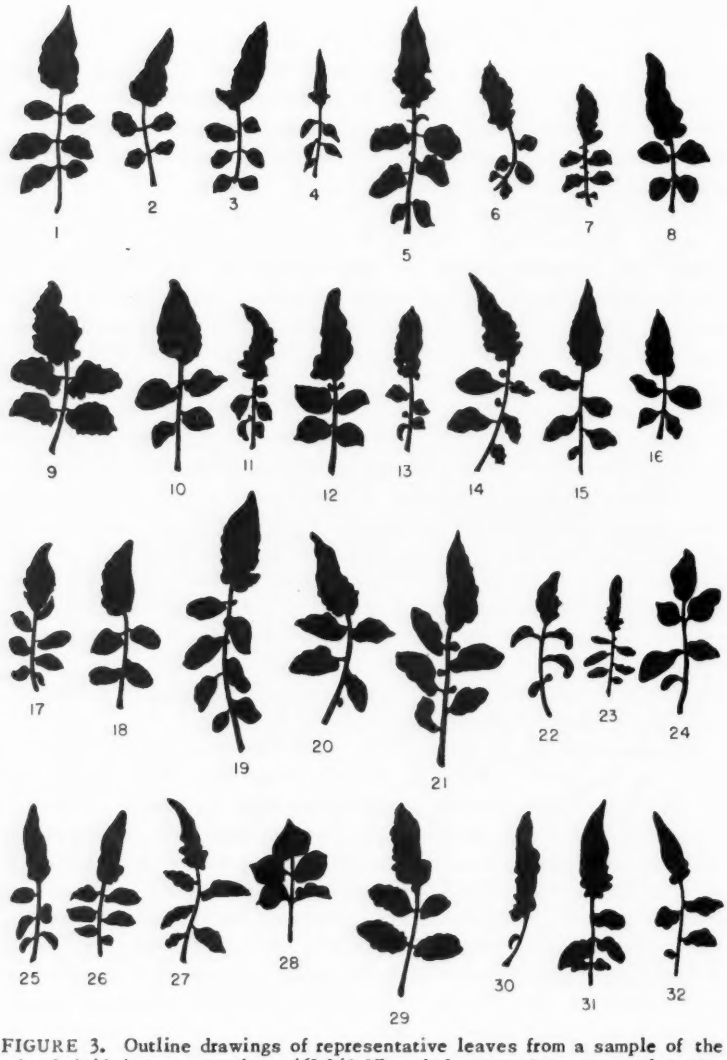

FIGURE 3. Outline drawings of representative leaves from a sample of the F_2 of the hybrid between variant 46L241-37 and *L. peruvianum* var. *dentatum* PI 128,657. Leaf No. 30 corresponds to the entire-leaf variant.

concluded that increased mutability accounted for the high proportion of variants he found in species hybrids of Antirrhinum.

In all of the examples encountered in this study the deviating condition behaved genetically as if determined by one or more recessive genes. The fact that the mutants appeared only in selfed progeny and not in descendents of two hybrids of different pedigree is compatible with the mutation hypothesis. If the mutations were gametic in origin, however, they must have oc-

curred at a very high rate. Assuming that each variant is conditioned by a single recessive gene—admittedly an oversimplification of the problem in the light of known facts—a minimum estimate of $\sqrt{2/46} = 21$ per cent is obtained for the gametic mutation rate. Compared with known normal and artificially accelerated mutation rates in other organisms, this is exorbitantly high and should lead to tremendous genetic instability.

Mutations occurring in the soma of the hybrid present a somewhat more plausible explanation. The chance that these would be transmitted to the F_2 would depend upon the stage of development at which they occurred and the part of the original plant from which cuttings were taken for clonal propagation, the earlier the mutation, the greater the probability of its survival. Somatic mutations of a rate of much lower order of magnitude could account for the observed results.

The absence of any dominant changes in the F_1 hybrids might argue against the somatic mutation hypothesis. In the course of these experiments the various F_1 hybrids have been maintained clonally for 4 to 10 years of culture as a large number of plants, each of which grew to very large size by the end of each summer season. Now, in the course of the many cell generations and great amount of material observed, the manifestation of dominant mutations with strong phenotypic effects would scarcely have been overlooked. Since, within the limits of observation, these clones have remained constant throughout the entire period of culture, it follows that dominant somatic mutations with marked phenotypic effects were very infrequent, probably no more frequent than in non-hybrid tomatoes.

In respect to the mutation hypothesis, therefore, gametic mutations are considered a highly unlikely source of the observed variants, and somatic mutations, although not by any means ruled out, a relatively unlikely source.

2. *Complementary action of genes of the parent species.* According to this proposal, normal alleles of each species interact in certain F_2 combinations to produce the variant phenotypes. In other words, the variants would be the manifestation of a form of transgressive segregation. The familiar example of novel variation in hybrids of *Antirrhinum majus* × *A. glutinosum* described by Lotsy (1916a) is commonly explained in this manner (Stebbins, 1950). After a systematic analysis of a variant in the same species hybrid, Mather and Vines (1951) arrived at a similar conclusion.

The statement of this hypothesis implies that variants should appear in progenies of hybrids of different combinations of the various biotypes of the two parental species. But this expectation is not realized in the present examples, for, while the two variants appeared in 46 F_2 plants of Hybrid No. 1 selfed, not one individual of either of the variant types or any other novel type appeared in 277 plants in the F_2 progenies of mixed parentage. In order to compare these two observed proportions statistically, Fisher's (1938) "exact treatment of 2 × 2 tables" was applied. The probability thus calculated that these two samples agree with each other is 0.0199. Complementary action as defined does not therefore likely explain the observations.

3. *Recessive genes derived from the self-incompatible parent.* The strict self-incompatibility of *L. peruvianum* (Lamm, 1950; McGuire, 1950) and *L. chilense* (Lamm, 1953) requires that these species reproduce in nature only by cross-fertilization. Recessive genes of low frequency consequently would seldom be fixed in homozygous condition and would usually exist in the population in the "latent" heterozygous form, their phenotypic expression being masked by normal alleles. The absence of the variant phenotypes in the observed populations of the self-incompatible parents, which were obtained from seeds collected in the wild, might therefore be deceiving and does not prove that the responsible genes were not present. On the other hand, although these genes would not likely become fixed in the parent species, the opportunity becomes much greater when they are transferred to species hybrids that can be self-pollinated. Hybrid No. 1 of the present series tolerated selfing, albeit at a very low frequency, and the cited Antirrhinum hybrid is self-compatible, the self-incompatibility behaving in a recessive manner in the hybrid.

Of the three proposed hypotheses, this is the only one that is completely in agreement with observed facts and deductions. It explains why variants appeared only in the progeny of the selfed hybrid. It requires no special assumptions and is in keeping with the known compatibility relations of the material. Furthermore, evidence to be presented proves that *L. peruvianum* and *L. chilense* harbor many other recessive genes of drastic effect, which can be revealed by inbreeding.

The acid test of the hidden-gene hypothesis is to demonstrate the presence of the recessive gene in the self-incompatible parent. Unfortunately the responsible genes derived from Hybrid No. 1 could not properly be analyzed in this fashion since the parent plant of *L. peruvianum* had been lost and very little stock of the original accession remains. Nevertheless, the opportunity for such a test was provided in the case of a new mutant of different parentage, the analysis of which is described in the following section.

VARIANT FROM HYBRID NO. 3

52L675-3 *Old-gold corolla.* The recent success in obtaining hybrids of group 3 between *L. esculentum* and *L. chilense* permitted tests not only of the hybrids, but parents as well. In a small F_2 population of 15 plants derived from a cross of two of these hybrids, a single plant was encountered which differed qualitatively from the remainder of the population in having a strong flush of dull orange color on the corolla and anthers. This coppery or tawny tone is entirely new, so far as the writers are aware, for either parent species, or, in fact, for any other lines that we have seen in the genus Lycopersicon. Even under the very high light intensity of midsummer in central California the difference between the flower color of this mutant and the normal yellow color is maintained until the corollas wither and shed (fig. 4), although the color becomes darker and the difference greater at other seasons of the year. Evidence as follows substanti-

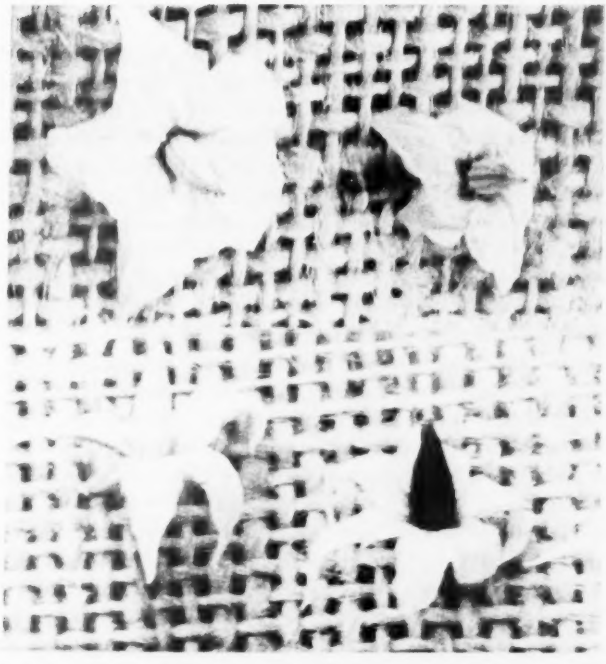

FIGURE 4. Representative flowers from mutant and normal tomatoes. Upper left, normal *L. chilense;* upper right, old gold, 52L675-3; lower left, normal *L. esculentum;* lower right, variant with brown anthers, LA 214.

ates that this deviation, in flower color, hereafter designated "old gold" is conditioned by a single recessive gene (*og*).

The availability of the parent plant of *L. chilense*, No. 4-32, permitted the critical tests of the origin of *og*, which could not have been made with the previously described mutants. As a test of the presence of *og* in the *chilense* parent, a backcross was made between the latter and one of the F_1 hybrids that yielded the segregating F_2. The progeny included 32 normal and 9 *og* plants, the segregation being so distinct that several inexperienced observers were readily able to classify the plants into *og* and + groups. The proportions are in keeping with those expected of an F_2 obtained by crossing two heterozygotes, but of much greater significance is the fact that the *og* gene was thus proved to exist in the self-incompatible parent.

Even though the data thus far presented argue in favor of the hidden-gene hypothesis, it is conceivable that complementary gene action of some sort between *og* and genes derived from *L. esculentum* might be necessary for the observed phenotypic expression.

The simple test to determine the expression, if any, of *og* in pure *chilense* background was then performed. The parent plant of *L. chilense* (4-32) was bred with a plant of another accession of the same species (LA 130, collected near Moquegua, Peru), three F_1 plants of this parentage being subsequently backcrossed to the original 4-32. Each of the three backcross families thus produced segregated for normal and old gold corolla color, the latter appearing undiminished in intensity. The total segregation in all families was 33+ : 7*og*. It is thus proved that *og* is expressed in the *chilense* parent as well as in the *esculentum-chilense* hybrids.

The totals of all segregating populations are 79+ and 17*og*. Although the number of *og* segregates is somewhat deficient, the deviation is not significant at the five per cent level. The available data therefore do not disprove the single recessive gene hypothesis.

Since *og* is expressed in approximately the same degree in pure *chilense* background as in the interspecific F_2, the expression of this gene does not seem to be modified appreciably by genes of *L. esculentum*. A final statement concerning complementary action cannot be made, however, until *og* has been transferred by backcrossing into a genotype that is nearly pure *L. esculentum*.

Summarizing all of the evidence, it has been demonstrated that the old-gold phenotype is the manifestation in homozygous condition of a single recessive gene *og* and that this gene was derived from *L. chilense*, in which parent species the *og* phenotype is not ordinarily found because the dominant allele is usually present, the heterozygous condition being promoted by the strict self-incompatibility of this species. Mutations resulting from species hybridization are not involved, and interaction of parental genotypes or cytoplasms is not necessary for the phenotypic expression of *og*; in fact, according to present limited evidence, such interaction seems not to amplify or diminish the expression.

Considering that the mutants having compound inflorescence and entire leaf behaved in parallel fashion in all investigated aspects, it is suggested that these might also be conditioned by recessive genes of the self-incompatible parent rendered homozygous by the self-pollination that obtained in the F_1 hybrid.

ADDITIONAL MUTANTS DERIVED FROM L. PERUVIANUM AND L. CHILENSE

A fourth mutant (LA 214) characterized by the striking dark pigmentation of its anther tubes (fig. 4) was recently encountered in a derivative of Hybrid No. 1. It did not appear in the F_2, but in a line that had been backcrossed from the hybrid to *L. esculentum* for several generations followed by one generation of selfing. At present nothing more is known about the inheritance of this condition except that it is recessive. This mutant provides another example, the known genetic facts about which could be explained by the hidden-gene hypothesis.

If all of the aforementioned freaks were derived ultimately from the self-incompatible parent, it follows that the latter species harbor a high concentration of recessive mutations in heterozygous condition. Although these species are not well known genetically, the few available facts seem to bear out this expectation. Within the species *L. peruvianum* and *L. chilense* four additional different mutants have been revealed as a result of inbreeding. (1) A mutant with dialytic anthers that is identical in phenotype with the *dl* of *L. esculentum* (Rick, 1947) was discovered by McGuire (1950) in the progeny of a sib mating of two plants derived from the cross of *L. peruvianum* PI 126,431 × PI 128,657. Although the family was very small, the segregation into five dialytic and nine normal plants hints that a single gene might be responsible for the deviating condition. (2) A completely sterile mutant with leaf-like calyx and corolla was discovered by Lamm (1953) in the progeny of a sib cross of plants of the *peruvianum* collection PI 128,657. The segregation of 35 normal and 15 mutant plants again points strongly to a single recessive gene. (3) The third mutant, a weak, partly chlorophyll-deficient plant, appeared in the progeny of a sib cross of *L. peruvianum* PI 126,944 in cultures at Davis. The segregation, 17 normal : four mutant, also fits a monogenic ratio. (4) The sticky-chromosome condition observed by Lesley and Lesley (1943) in Holmes' (1939) collection of *L. dentatum* (likely *L. chilense*) may also belong in this group. Two of three plants presumably derived by self-pollination of the original plant obtained by Holmes displayed this chromosome abnormality and attendant sterility.

It is noteworthy that so many of the mutants obtained within the species *L. peruvianum* or from hybrids with *L. esculentum* trace to the collection PI 128,657 of the former species. The concentration of recessive mutants in this collection may point to some unusual condition. On the other hand, in view of the fact that it has been investigated to a greater extent, possibly as a result of Smith's (1944) success in obtaining a hybrid between it and *L. esculentum*, it is considered more likely that this collection is typical of the species as a whole.

If these few examples characterize *L. peruvianum* and *L. chilense*, these species must be replete with recessive genes of major and dramatic effect, which can be expressed within the species after fixation by inbreeding and which might readily be recovered from hybrids between these species and *L. esculentum*.

NOVEL VARIATION IN OTHER SPECIES HYBRIDS

The aforementioned example, which is probably the best known and most frequently cited, is Lotsy's (1916a) *Antirrhinum rhinanthoides* obtained as a segregate in the F_2 of the hybrid, *A. majus* × *A. glutinosum*. The flowers of this mutant differed markedly from any type known in the parent species and from any other segregates in the F_2; in fact, they showed greater resemblance to flowers of the genus Rhinanthus than to those of any other form of Antirrhinum. Lotsy ascribed the origin of this mutant to something

intrinsic in hybridization and drew support from this example for his theory of evolution by hybridization (Lotsy, 1916b).

The case of *A. rhinanthoides* has been critically reviewed by Stubbe (1940), who had found a Mendelian recessive mutant in *A. majus*—"fistula"—having very similar floral morphology. He also studied hundreds of F_2 segregates of the same species hybrid without encountering any plants of the mutant type that would have been expected on the basis of Lotsy's premise. Stubbe therefore rightly concludes that the appearance of *A. rhinanthoides* was not invoked by hybridization *per se*, but that it more likely appeared as a result of fixation of a mutant gene that existed in heterozygous condition in one of the parent species. Since the *glutinosum* parent is self-incompatible, it might be ventured further that the gene in question existed in this species in the same fashion as *og* in *L. chilense* of the present investigation. Pertinent to this proposal is the following statement by Lotsy (1916b) concerning the parentage of his material: "As *A. glutinosum* contains several types, all of which are completely self-sterile, the F_1 generation obtained was somewhat polymorphous, though not to a considerable extent."

Attention should be called here also to the "cleistogamy" encountered in the same species hybrid by Mather and Vines (1951). Their extensive breeding tests indicate that the cleistogamous condition is inherited in complex fashion, several recessive genes exerting a supplementary effect, and expression is subject to considerable modification by environmental and developmental factors. Backcrosses to *A. glutinosum* revealed the presence of one or two of the responsible genes in that species. They indicate that "although floral abnormalities have been observed in inbred material (of *A. glutinosum*) nothing which could properly be termed cleistogamy has been seen in this species up to the present time," but also admit that sufficient numbers of this species had not been examined to rule out the possibility that it might have contributed all of the necessary genes, and that, consequently, the true cleistogamous condition might also appear within this parent.

Additional mutants derived from hybrids of *A. majus* and species of the *glutinosum* group are described by Baur (1932). He ascribes the origin of these new forms to increased factor mutability in the species hybrid.

Novel variations that might be explained by the hidden-gene hypothesis are not necessarily limited to species hybrids of Lycopersicon or Antirrhinum. Howard and Swaminathan (1952) point out that small and deformed plants that have been encountered by themselves and other workers in F_2 generations of hybrids of self-incompatible diploid species of Solanum might readily be explained in this manner. The segregation of numerous non-surviving dwarf plants in the F_2 of *Layia gaillardioides* × *L. hieracioides* described by Clausen (1951) also deserves mention here. The former species is self-incompatible, whereas the latter and the F_1 are self-fertile.

This mode of origin of novel variations might also apply to hybrids other than those of self-incompatible species. Many other devices such as the

dioecious condition promote outcrossing and thereby afford less opportunity for the fixation of genes. The anticipated high levels of cryptic variability have been found in many cross-fertilizing wild species; for example, species of Drosophila (Spencer, 1947).

What proportion of aberrant types in the progeny of species hybrids in general owe their origin to recessive genes derived from a highly cross-fertilized parent remains to be ascertained. We would be remiss, however, not to point out that other mechanisms have been demonstrated to be responsible for novel variation in certain hybrids. Complementary interaction of genes of parental species, for instance, must account for the extensive weakness and degeneration of the F_2 progeny of the hybrid, *Gossypium barbadense* × *G. hirsutum* (Harland, 1936). Interaction of the cytoplasm of one species and genes of another explains novel variation in other materials—for example the hybrids between various species of Epilobium (Michaelis, 1951) and Nicotiana (Clayton, 1950). The mutation hypothesis cannot yet be dismissed entirely from consideration, especially in the light of the increased frequencies of chromosome breakage that have been observed in species hybrids of Tradescantia (Giles, 1940) and Bromus (Walters, 1952).

Finally, in connection with the use of species hybrids in plant breeding, it should be pointed out that the appearance of novel variations, whatever their genetic basis, argues in favor of the exploratory use of F_2 generations instead of the exclusive practice of the backcross method. The opportunity for detecting novel variants, particularly those conditioned by recessive genes, is very much greater in F_2's than in the backcross method as usually practiced. The potential value of such variants is as difficult to predict as their appearance. Although no immediate practical value is known for the variants reported here, it is conceivable that useful types might appear in future cultures. Whatever agricultural value they might have, their unpredictable features and frequency lend additional fascination to the study of species hybrids and the moral stimulus thereby provided to the breeder should not be overlooked. For these reasons it would seem prudent to study at least to a limited extent the F_2 generation of species hybrids that are bred for plant improvement.

SUMMARY

Several novel variants that appeared in F_2 populations of hybrids between *L. esculentum* and the self-incompatible species *L. peruvianum* and *L. chilense* are described. The deviating phenotypic features of these variants are completely outside the normal range of variation of their respective F_2 families and were not known to be present in the parental species. Tests of inheritance, where performed, indicate that one or more recessive genes is responsible for the abnormal condition. Conclusive genetic evidence was obtained only for the variant having old-gold flowers derived from the hybrid of *L. esculentum* × *L. chilense*, indicating the action of a single recessive gene, *og*, of major effect. Appropriate test crosses demon-

strated that *og* is present in heterozygous condition in the *chilense* parent and that, furthermore, it gains phenotypic expression within that species equal to that in the F_2 or backcross with *L. chilense*. Information concerning the origin of the other novelties is not so conclusive, yet the available facts are in keeping with an explanation like that for *og*—namely, fixation, on selfing the F_1 hybrid, of recessive genes present in heterozygous form in the self-incompatible parental species. Limited experience in inbreeding *L. peruvianum* and *L. chilense* reveals a great wealth of recessive genes of major effect that would be expected on the basis of this hypothesis. For reasons presented, hypotheses based on high mutation rates induced by hybridity and on complementary interaction of normal alleles of the parents are considered less likely to explain the origin of the variants. Certain other instances of aberrant segregates in the F_2 of species hybrids reported in the literature might also possibly be explained by recessive genes derived from the self-incompatible parents.

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THE EFFECT OF COMPENSATION ON POPULATIONS SUBJECT TO NATURAL SELECTION

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One of the unresolved problems in the study of human populations is that of the remarkable polymorphism of man with respect to a large number of hereditary diseases. Considering the selection against these traits, it is difficult to explain their maintenance in the species without postulating abnormally high mutation rates or selection in favor of the heterozygotes, for which there is, as yet, no evidence. Of late, a new phenomenon has been noted which may play an important rôle in human polymorphism. That phenomenon is compensation. Compensation may be defined simply as an increase in the average number of children conceived by parents who have had children affected by an hereditary disorder. At the moment it is not clear whether such compensation takes place only in families where defective offspring have died, or whether it is equally applicable to families having living debilitated children. The data of Glass (1950) on erythroblastosis foetalis due to Rh incompatibility, and those of Race (1942) on acholuric jaundice, both show clear evidence of compensation.

It is to Li (1953) that we owe a clear, simple, and workable quantification of this effect. Using his method of attack it is a simple matter to investigate the effect of compensation on various modes of selection. As Li has shown, the effect of this phenomenon in the case of selection against the heterozygote is simply to change the unstable equilibrium point, the final effect being the same as without compensation.

It is the purpose of this paper to show the result of compensation in the case of selection against a recessive and that against a dominant.

GENERAL CONSIDERATIONS

Li's compensation coefficient, t, may be calculated either from the total number of pregnancies in a given mating or from the number of *living* children only. In the latter case a correction must be made. In all that follows, matings which are genotypically capable of producing affected offspring will be called "susceptible matings." Now it is clear that a susceptible mating will show compensation even if the average family size is the same as for non-susceptible matings, since the effect of selection is to cut down on the average number of living children. Two measures of compensation may be calculated as follows, where t is the compensation coefficient, s the selection coefficient, and $q = 1 - p$ is the frequency of the recessive gene:

$$(1) \qquad 1 + t = \frac{\text{average number of pregnancies in susceptible matings}}{\text{average number of pregnancies in non-susceptible matings}}$$

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$$(2)\quad 1 + t^* = \frac{\text{average number of living children in susceptible matings}}{\text{average number of living children in non-susceptible matings}}$$

where

$$(3)\quad 1 + t = \frac{(1 + t^*)(1 - q^4)}{(1 - s)(1 - q^2)}$$

for the case of selection against a dominant and

$$(3a)\quad 1 + t = \frac{(1 + t)[1 - p^2(2 - p^2)]}{(1 - s)\,q^2}$$

for the case of selection against a recessive.

Equations (2), (3) and (3a) are only approximations since they assume that selection is entirely confined to infant mortality or abortion. This is untrue in many cases, so that s in these equations must be regarded as an underestimate of the selection coefficient. The data available may be directly useful only for calculating t^* but equations (3) and (3a) may be used to get t, this latter quantity being used in the following calculations.

SELECTION AGAINST A DOMINANT

In the case of a complete dominant all marriages involving genotypes AA or Aa are susceptible matings. The assumption is that compensation and selection are the same for both genotypes. This is admittedly an oversimplification of the model for many cases, but in the absence of any evidence to the contrary these assumptions will be considered valid. Allowing s, t and q to have the meanings already assigned to them, the outcomes of the various matings are given by table 1.

TABLE 1

RELATIVE FREQUENCY OF OFFSPRING AFTER SELECTION AGAINST THE DOMINANT AND COMPENSATION

Mating	Offspring		
	AA	Aa	aa
AA × AA	$p^4(1 - s)(1 + t)$		
AA × Aa	$2p^3q(1 - s)(1 + t)$	$2p^3q(1 - s)(1 + t)$	
Aa × Aa	$p^2q^2(1 - s)(1 + t)$	$2p^2q^2(1 - s)(1 + t)$	$p^2q^2(1 + t)$
Aa × aa	....	$2pq^3(1 - s)(1 + t)$	$2pq^3(1 + t)$
aa × aa	....	....	q^4
AA × aa	....	$2p^2q^2(1 - s)(1 + t)$	....
Total	$p^2(1 - s)(1 + t)$	$2pq(1 - s)(1 + t)$	$q^2[1 + t(1 - q^2)]$

In the absence of selection and compensation, the expected frequencies of homozygous dominant, heterozygous, and homozygous recessive offspring are, respectively, p^2, $2pq$, and q^2. The totals in table 1 show that after selection and compensation each of the above expected values is multiplied by a function of s, t, and q or some combination of these. These multipliers

are the relative adaptive values, representing simply the proportion of the expected frequencies which are present after compensation and selection.

Denoting the adaptive values by W with the appropriate subscript the totals in table 1 give:

$$W_{AA} = W_{Aa} = (1 - s)(1 + t) \tag{4}$$

$$W_{aa} = 1 + t(1 - q^2) \tag{5}$$

The frequency of the recessive allele, then, will increase if:

$$W_{aa} > W_{Aa} = W_{AA} \tag{6}$$

while it will decrease if:

$$W_{aa} < W_{Aa} = W_{AA} \tag{7}$$

These conditions may be written using (4) and (5) as:

$$\text{Increase of } a\text{:} \qquad \frac{s(1 + t)}{t} > q^2 \tag{8}$$

$$\text{Decrease of } a\text{:} \qquad \frac{s(1 + t)}{t} < q^2 \tag{8a}$$

with the result that the equilibrium at:

$$\sqrt{\frac{s(1 + t)}{t}} = \hat{q} \tag{9}$$

is a *stable* one. Had the inequalities in (8) and (8a) been reversed, the equilibrium would have been unstable. In order for $\hat{q}$ to lie strictly between zero and unity it is necessary that

$$\frac{s(1 + t)}{t} < 1,$$

which is equivalent to requiring that

$$t > \frac{s}{1 - s}. \tag{10}$$

A specific case may be examined using the data of Race (1942) on acholuric jaundice. Table 2 gives the pertinent information. Using the total number of children per parent, that is, both living and dead, equation (1) yields

$$t = 1.06.$$

At present the selection against acholuric jaundice is not known, but if the present frequency of the recessive trait is assumed to be the equilibrium value, ($q = .99$), then equation (9) may be solved for the value of s. This gives

$$s = .51.$$

TABLE 2

FERTILITY OF PERSONS AFFECTED BY ACHOLURIC JAUNDICE AND THEIR NORMAL SIBS (RACE, 1942)

Parents	Offspring		
	Alive	Dead	Total
21 affected persons	37	18	55
15 non-affected sibs	19	0	19
10 affected males	21	4	25
6 normal sib males	12	0	12
11 affected females	16	14	30
9 normal sib females	7	0	7

Another estimate of the selection against this trait can be obtained from the infant mortality data given in table 2. This gives a value of $s = .64$, which considering the small sample is fairly good agreement between the two estimates.

SELECTION AGAINST A RECESSIVE

Following the same method as for the case of a dominant trait, table 3 was constructed to show the outcome of various matings. The adaptive values of the three genotypes are then:

(11) $$W_{AA} = 1 + tq^2$$

(12) $$W_{Aa} = 1 + tq$$

(13) $$W_{aa} = (1 + t)(1 - s)$$

Now clearly $W_{Aa} > W_{AA}$ for all non-trivial values of q and t. There then remain two possible relations among the three adaptive values:

(14) $$W_{aa} \gtrless W_{Aa} > W_{AA}$$

or

(15) $$W_{aa} < W_{Aa} \quad \text{and} \quad W_{AA} < W_{Aa}$$

TABLE 3

RELATIVE FREQUENCY OF OFFSPRING AFTER SELECTION AGAINST THE RECESSIVE AND COMPENSATION

Mating	Offspring		
	AA	Aa	aa
AA × AA	p^4	....	....
AA × Aa	$2p^3q$	$2p^3q$	....
Aa × Aa	$p^2q^2(1 + t)$	$2p^2q^2(1 + t)$	$p^2q^2(1 + t)(1 - s)$
Aa × aa	....	$2pq^3(1 + t)$	$2pq^3(1 + t)(1 - s)$
aa × aa	....	....	$q^4(1 + t)(1 - s)$
AA × aa	....	$2p^2q^2$	....
Total	$p^2(1 + tq^2)$	$2pq(1 + tq)$	$q^2(1 + t)(1 - s)$

Relation (14) will result in an increase in the frequency, q, of the recessive allele. Using relations (12), (13) and (14) this may be written as: a increases if

$$(16) \qquad (1+t)(1-s) \gtrless 1+tq$$

i.e.

$$(17) \qquad q \lessgtr \frac{t-s(1+t)}{t}$$

Condition (17) means simply that the recessive allele is prevented from being lost. This does not mean that q increases until it reaches unity for when

$$(18) \qquad q > \frac{t-s(1+t)}{t}$$

condition (15) is seen to hold, that is the heterozygote is superior to either homozygote. In such a case a stable equilibrium will be reached at the value

$$\hat{q} = \frac{X}{X+Y}$$

where $X = W_{Aa} - W_{AA}$ and $Y = W_{Aa} - W_{aa}$
For the case in question

$$(19) \qquad \hat{q} = \frac{t\hat{q}^2 - t\hat{q}}{t\hat{q}^2 + t - s(1+t) - 2tq}$$

Solving for q,

$$(20) \qquad \hat{q} = \frac{3t \pm \sqrt{9t^2 - 4t[2t - s(1+t)]}}{2t}$$

Like equation (10), equations (17) and (20) do not have biologically meaningful solutions for all values of s and t. Biologically meaningful solutions must satisfy the relation

$$(21) \qquad 0 \lessgtr \hat{q} \lessgtr 1,$$

which implies that q must be real. In all that follows, the case where t is negative will be distinguished from that in which t is positive. By definition t may be as small as -1. When t is negative, we do not have compensation, strictly speaking, but its reverse. Nevertheless, in the interests of generality it is well to examine such cases.

For q to be meaningful in equation (17) it is necessary that

$$(22) \qquad 1 \gtrless \frac{t-s(1+t)}{t} \gtrless 0 \quad (t>0),$$

that is

$$(23) \qquad t \gtrless \frac{s}{1-s}$$

TABLE 4

LIMITS OF t FOR VARIOUS VALUES OF s WHICH ALLOW OF MEANINGFUL SOLUTIONS OF EQUATIONS (9), (17) AND (20)

s	Eq. (9), (17) $t >$	Eq. (20) $t >$
1.00		1.00
.90	9	.82
.80	4	.67
.75	3	.60
.74	2.85	.59
.50	1	.33
.40	.66	.25
.30	.33	.18
.10	.11	.05
.00	.00	.00

The values satisfying inequality (23) which are identical with those given by (10), are shown in table 4. When t is negative, however, the condition for a meaningful q is

$$t < -1 \tag{24}$$

which is impossible by definition.

In order that $\hat{q}$ is defined by equation (20) will lie strictly between zero and unity, it is necessary that:

$$3t > \sqrt{9t^2 - 4t[2t - s(1 + t)]}\ (t > 0) \tag{25}$$

Solving for t, this gives

$$t > \frac{s}{2 - s} \tag{26}$$

Since s must lie between zero and unity, only positive values of t will allow q to lie strictly between zero and unity. In deriving (26) from (25) it was necessary to square the expression under the radical. This allows imaginary roots if only condition (26) is satisfied. To eliminate such imaginary roots, it is necessary to make the further restriction that:

$$9t^2 \geqslant 4t[2t - s(1 + t)] \tag{27}$$

and solving for t

$$t \geqslant \frac{-4s}{1 + 4s}\ (t > 0) \tag{28}$$

which is true by definition.

Sample values of (26) have been tabulated in table 4. An inspection of the table and the previous results give the following conditions for equilibrium:

(1) If t is negative or zero, the recessive deleterious gene is eliminated.

(2) If t lies strictly within the limits in table 4 for each value of s shown, there will be an equilibrium with both types present.

(3) The lower limit of t for each value of s is smaller in equation (20) than in (17). This assures that if an equilibrium is possible, the value of q will reach the range within which the heterozygote is superior.

Since the conditions given by equation (10) for a non-trivial equilibrium for the case of selection against the dominant are identical with the conditions for a solution of eq. (17), table 4 does not make a distinction between these cases.

Compensation, then, has definite qualitative results in selective systems. Without compensation, selection against a dominant or recessive results in the eventual elimination of the allele under selection. Compensation may allow of stable equilibria in both these cases, thus preserving the polymorphism of the population.

It is impossible to say at this point how widespread a phenomenon compensation is, but it is clear that it may be a potent evolutionary force.

SUMMARY

The result of compensation in family size has been investigated, both for the case of selection against a dominant and recessive. In both cases a stable equilibrium may result. The range of values of compensation and selection for which equilibria do result has been shown.

The methods developed are used to estimate the strength of selection in the specific case of acholuric jaundice.

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ON THE INABILITY OF ANTIBODIES TO INDUCE MUTATIONS IN BACTERIA*

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Sturtevant (1944) has proposed that, since the specificity of an antigen is genetically determined, gene and antigen may have identical surfaces. In this case antibodies developed against an antigen could combine with the corresponding face of the gene and, in so doing, produce a mutation at the time of gene reproduction. Emerson (1944) has tested this suggestion with antisera against *Neurospora crassa* and has reported the induction of rather nondescript mutants. Unfortunately, the instances of exposure to normal serum, which were the only true controls, were not numerous enough to determine whether there was a significantly different number of mutants among the experimentals. The same is true of the results of Andersson-Kottö (1951), while Fox and Ziebur (1952), working with similar systems, reported results which were clearly negative. If all of these experiments in reality yielded negative results they would still not constitute an adequate test of the hypothesis because the antisera were produced against whole mold or culture filtrate and it was not known that there was a high titer against any one antigen present. As a matter of fact, the above-mentioned investigators could not detect antigenic differences between the parents and the mutant strains found. It seemed desirable, therefore, to perform experiments with antisera known to have a high titer against some one antigen whose presence or absence could be readily determined in the cell.

For this purpose, antibodies against the enzyme β-galactosidase (lactase) were used. This enzyme, found in traces in lactose-non-utilizing (lac^-) *Escherichia coli* and in unadapted lactose-utilizing mutants (lac^+), is formed in large amounts in lac^+ bacteria adapted by growth in the presence of lactose or related compounds (Monod and Cohn, 1951). Antibodies, formed against the enzyme and purified, specifically precipitate the enzyme (G_Z) and a related protein (P_Z) (Cohn and Torriani, 1953). They will also distinguish between lac^- or unadapted lac^+ and adapted lac^+ bacteria by agglutinating the latter at a dilution between one half and one fifth that required to achieve just detectable agglutination of the former. The lac^- and unadapted lac^+ bacteria can be agglutinated, despite the fact that they contain only about 5×10^{-4} of the β-galactosidase of adapted lac^+ bacteria, presumably because they do contain P_Z protein. Their total combining antigen ($P_Z + G_Z$) is, however, between one half and one fifth that of adapted lac^+ bacteria (Cohn and Torriani, 1953).

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The γ-globulin antienzyme, the normal γ-globulin and the β-galactosidase used in these experiments were kindly supplied by Dr. Melvin Cohn. The antienzyme had been prepared by the injection into rabbits of purified β-galactosidase from fully adapted *Escherichia coli* ML. The resulting antiserum was then absorbed by extracts of unadapted bacteria known to contain little or no enzyme. This removed all antibodies except those specific for β-galactosidase and P_Z protein. The γ-globulin fraction was prepared by Dr. Cohn and, upon receipt, was titrated with β-galactosidase by the procedures referred to in Cohn and Torriani (1952). The dose used in these experiments was 500 enzyme equivalents per 2 ml. of bacterial suspension, which contained ca. 5×10^8 bacteria in stationary phase experiments or an initial number of ca. 5×10^6 bacteria in experiments involving bacterial growth. This amount of antienzyme is equivalent to the amount of β-galactosidase in 5×10^8 fully adapted bacteria grown on lactose. Since the bacteria used were grown on glucose and unadapted, they contained amounts of β-galactosidase equivalent to either 5×10^{-4} or 5×10^{-6} of the antienzyme employed; their content of total combining antigen was the equivalent of either about one half or one two hundredth of the antienzyme. Although sterile procedure was used throughout, the γ-globulins were never sterilized. They were, however, prepared aseptically and were centrifuged at about 5000 r.p.m. for one half hour before use and were kept frozen in the interim. In the course of these experiments the anti-β-galactosidase activity of the γ-globulin antienzyme was found not to have changed.

Although a variety of different combinations of treatment were used the basic procedure was the same. Both lactose-utilizing (lac^+) and non-utilizing (lac^-) strains of *Escherichia coli* ML were employed as test organisms. The culture conditions and methods of detecting mutants of different lactose fermenting character have been described elsewhere (Ryan, 1952). In addition, an attempt was made to concentrate lac^- bacteria among lac^+ by the use of penicillin. The medium consisted of the minimal solution of salts with 0.2 per cent lactose and was previously cleaned of carbon source by sterile filtration some 24 hours after it had been inoculated with a washed suspension of lac^- bacteria. A thousand-fold concentration of lac^- mutants was sometimes achieved with 150 units of penicillin per ml. despite the fact that control experiments showed that only about 1 per cent of the added lac^- bacteria survived the treatment. This method was never used by itself but the treatment being tested was always repeated in an experiment where the lac^- mutants were measured in each case by the direct plating of a total of between 2×10^4 and 1.5×10^5 bacteria on a large number of indicator agar plates.

When bacteria were treated in the stationary phase, 1 ml. of an overnight culture grown in glucose-minimal medium and containing about 5×10^8 organisms, was mixed with 1 ml. of buffer containing 500 enzyme equivalents of the γ-globulin antienzyme and rolled in a test tube for aeration at 37°C. for 12 hours. Controls consisted of bacteria treated similarly with normal γ-globulin and with buffer alone. A very slight agglutination of the bacteria

being treated, detectable only under the microscope, was observed in the γ-globulin antienzyme. The clusters were dispersed, however, by the dilution and spreading. Bacteria treated during growth were diluted in a minimal medium with 0.05 per cent glucose so that, when 1 ml. of the suspension was mixed with 1 ml. of buffer or of either γ-globulin, about 7 generations of growth ensued. When other treatments were also used, growth at 37° in rolled tubes was first allowed to occur for about 6 generations in the γ-globulins or buffer mixed with minimal medium and 0.05 per cent glucose. Then, for example, the culture was exposed to ultraviolet light in an open petri dish rotated under a Westinghouse Sterilamp. Precautions to prevent photoreactivation were taken. The treated culture was either reincubated directly, or, after centrifugation, was resuspended in fresh medium with the original supplements. The number of generations that followed this treatment was a function of the amount of killing, and after the two doses of ultraviolet light used was either about 6 or about 14 generations. The infra red treatment was carried out for 3 hours at 18°C. according to the method of Swanson (1949) and, since no death occurred, was followed by about two generations of growth in the original solutions. Exposure to a 0.2 per cent solution of nitrogen mustard [methyl-bis-(β-chlorethyl) amine hydrochloride] in buffer and 2 per cent sodium chloride, for one half hour, was always followed by washing and resuspending in solutions like the original where about 11 generations of growth occurred.

In the case of mutations from the lac^- to the lac^+ condition the γ-globulin antienzyme did not influence the number of mutants irrespective of whether the treatment was combined with ultraviolet, infra red or nitrogen mustard (table 1). The numbers of lac^+ mutants found among the experi-

TABLE 1

MUTANT FREQUENCY AFTER VARIOUS TREATMENTS OF *Escherichia coli* ML WITH γ-GLOBULIN ANTI-β-GALACTOSIDASE.

Accessory Treatment	$lac^+ \longrightarrow lac^-$ ($\times 10^{-5}$)			$lac^- \longrightarrow lac^+$ ($\times 10^{-6}$)		
	Buffer	Normal γ-globulin	γ-globulin antienzyme	Buffer	Normal γ-globulin	γ-globulin antienzyme
None, stationary phase	< 1.3	1.8	<40	....	1.8	3.0
None, stationary phase (penicillin)	12.0	<1.3	< 1.3	....	....	....
None, growing bacteria	< 3.1	<4.8	< 6.2	3.3	4.2	4.5
None, growing bacteria (penicillin)	< 1.3	<1.3	< 1.3	....	....	....
Ultraviolet, ca.10^{-2} survival (penicillin)	2.0	0.83	0.65	1.2	2.3	3.0
Ultraviolet, ca.10^{-5} survival	....	....	2.1	....	....	2.4
Infra red	....	1.0	1.9	....	5.0	15.0
Nitrogen mustard, ca.10^{-4} survival	....	5.2	2.4	....	4.5	2.9

mentals and their controls had an average frequency of 3.2×10^{-6}. An exceptional value of 15×10^{-6}, found after the combined treatment of γ-globulin antienzyme and infra red, is not included in this average because, in view of the errors inherent in such determinations, it is not considered to be indicative of a real biological difference.

Similarly, the γ-globulin antienzyme was inactive, both by itself and in combination with the other treatments, with regard to mutations from the lac^+ to the lac^- condition. When the variable results obtained after penicillin treatment, which in themselves did not indicate a mutagenic effect, were omitted, the average frequency of lac^- mutants among controls and experimentals was 2.5×10^{-5}. In a separate and different experiment, where adapted lac^+ bacteria were allowed to grow for 7 generations and to remain about three hours in the stationary phase in medium containing lactose instead of glucose, the γ-globulin antiserum was similarly without effect. In the presence of lactose and 1.5×10^4 enzyme equivalents of the γ-globulin antiserum (equal to three thousand times the total combining antigen in the bacteria at the beginning of growth or thirty times that in the bacteria in the stationary phase) the frequency of lac^- mutants was $<6.3 \times 10^{-6}$; in the presence of lactose and equivalent amounts of normal γ-globulin the lac^- frequency was $<2.8 \times 10^{-6}$.

DISCUSSION

It can then be concluded that these experiments with antibodies did not yield evidence of their mutagenicity. The antibodies did not interfere with the multiplication or stability of either the genes enabling lactose utilization in lac^+ bacteria or the genes preventing lactose utilization in the lac^- strain. Nor did other treatments show a clear mutagenic effect either by themselves or in combination with γ-globulin antienzyme. These experiments may have given negative results for other reasons than that there is no structural relationship between the gene and the enzyme whose synthesis it controls. Although the antibodies had a demonstrable reactivity with the bacterial β-galactosidase, whether they penetrated the bacteria is a question difficult to answer. The methods used by Coons (1953), Gitlin et al (1953) and by Crampton and Haurowitz (1950), which enabled the demonstration of the penetration of antigens and antibodies into the nuclei of mammalian cells, cannot be directly applied to bacteria. Furthermore, the similarity between the gene and its enzyme may not in the case investigated involve the antigenic sites of the enzyme. In this connection it might be noted that the enzymatic activity of bacterial β-galactosidase does not depend upon the sites that combine with antibodies (Cohn and Torriani, 1952).

Nevertheless, the continued demonstration of the lack of mutagenicity of antibodies should not be minimized by the compounding of hypotheses. More general considerations of the problem of the induction of specific mutations (Emerson, 1945; Monod, 1947) indicate that, if the gene and its enzyme have similar properties, mutations might be induced by enzyme inhibi-

tors and substances with affinity for the enzyme. Tests of this possibility have also yielded negative results. The non-mutagenicity of certain compounds with an affinity for bacterial β-galactosidase, already demonstrated for strain ML (Ryan, 1952), has been confirmed with strain K 12 of *E. coli*. M/1000 D-galactose, methyl-β-D-galactoside and phenyl-β-D-thiogalactoside did not result in the appearance of more lac^- mutants ($< 2 \times 10^{-5}$) among lac^+ bacteria than were found in their absence.

There still does exist a case in which the induction of specific mutations remains a definite possibility. Wright (1951, 1953) has evidence which indicates that some α-hydroxy acids specifically increase the number of reversions in a glycineless mutant of *E. coli*. Inasmuch as Wright herself has presented a number of reservations which must be held in this case, it would seem that a fruitful approach to the problem of the induction of specific mutations is not yet available. Either the existing theoretical considerations have been too naïve or new practical methods must be devised to expose the gene to its environment.

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LIGHT AS AN ECOLOGICAL DETERMINANT OF INTERSPECIFIC COMPETITION BETWEEN *DROSOPHILA WILLISTONI* AND *DROSOPHILA MELANOGASTER*

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Most of the observations on animal behavior in response to light deal with the movement of individuals with relation to a light source, the influence of intensities and different kinds of light, and the mechanisms or sensory organs whereby animals respond to light (Mast, 1911; Fraenkel and Gunn, 1940). Few studies, however, indicate the possible role of light in the determination of the ecological niche of the species. It was noticed in a fingerbowl containing two species of Drosophila that the larvae of each species had pupated in different regions of the fingerbowl. Preliminary studies indicated that this differential distribution of the pupae was due to light intensity and not humidity and thickness of the food.

MATERIALS AND METHODS

Covered glass dishes 20 × 10 × 5 cm. were prepared with a two centimeter layer of cream of wheat-molasses food (Spassky, 1943). Food dishes were placed under boxes which were located equidistant from a source of light (fig. 1). The experimental dishes were illuminated through a milky glass window 6 × 6.5 cm. in the box while the control dish remained in a light-tight box. The first experiments were conducted at room temperature (23°—25° C) with a 60 watt bulb at a distance of 30 cm. from the boxes as a light source. In later experiments the whole set-up was transferred to a basement room with a temperature of 18°—20° C, and the light source was placed in a beaker immersed in a trough of running water. The temperature of the food in the end of the dish closest to the light source and at the opposite end of the dish were recorded simultaneously by using two standardized thermometers. No perceptible differences were noted.

D. willistoni (Standard) and *D. melanogaster* (Oregon-R) were used in this study. Eggs were placed at the midline of the dish, and counts of the distribution of the pupae were made after all of the larvae had undergone pupation. The dish was divided into quarters for counting in addition to the front and back glass panels of the dish. In the earlier experiments, however, the pupae on the front glass panel were included in the count of the first quarter and the pupae on the back glass panel were included in the fourth quarter.

RESULTS

The data in table 1, Experiments A and B, are samples of the series of experiments run at room temperature and at lower temperatures respectively.

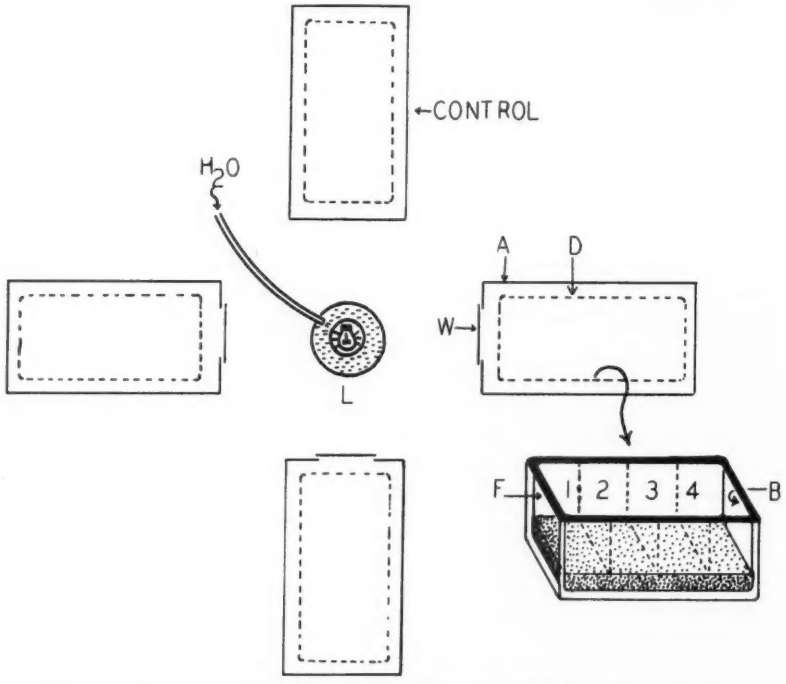

FIGURE 1. Method of examining the preference for light intensity. D, covered glass dish; A, box; L, light source; W, window with milky glass; F, glass panel closest to light; B, glass panel opposite F; 1,2,3,4, quarters of the dish numbered such that 1 is closest to the light source and 4 is the most distant from the light source; Control, light-tight box.

For statistical treatment the data have been combined in such a manner that the two halves of the dish are compared. This method was considered advisable to rule out any factors, such as preference to pupate on food or glass, which may vary among the quarters. Thus the only variable between the two halves of the dish is the light intensity. The comparison of the distribution of pupae is based on the assumption that the larvae may go either toward the light or away from the light at random provided there is no bias introduced by light. The probability that a larva will pupate in either half of the dish is 0.5. The data were thus tested for fit to a 1 : 1 ratio.

There is a random distribution of the pupae of *D. melanogaster* in the control dish in Experiment A, whereas a significant deviation from a 1 : 1 ratio occurred in the illuminated dish. The larvae of *D. melanogaster* when exposed to the light conditions of the experiment tended to pupate away from the light source.

In Experiment B eggs of *D. melanogaster* and *D. willistoni* were placed in the same dish and observed simultaneously with dishes which contained

TABLE 1

PREFERENCE FOR LIGHT INTENSITY OF DROSOPHILA LARVAE

Experiment A at Room Temperature 23°—25° C							
		(1)	(2)	(3)	(4)		Total
D. melanogaster		10 +	32 = 42	87 +	219 = 306		348
Control		48 +	68 = 116	35 +	66 = 101		217
Experiment B at Temperature 18°—20° C.							
	F	(1)	(2)	(3)	(4)	B	Total
D. melanogaster	87 +	94 +	145 = 326	139 +	195 +	196 = 530	856
D. willistoni	75 +	153 +	109 = 337	130 +	82 +	19 = 231	568
Competition Experiment:							
D. melanogaster	63 +	77 +	44 = 184	95 +	197 +	207 = 499	683
D. willistoni	29 +	44 +	37 = 110	15 +	4 +	3 = 22	132
Control: mixture of:							
D. melanogaster	125 +	88 +	97 = 310	93 +	103 +	111 = 307	617
D. willistoni	10 +	60 +	34 = 104	39 +	47 +	19 = 105	209

(1), (2), (3), (4), consecutive quarters of the food dish with (1) closest to the light source; F, glass panel of the dish closest to the source of light; B, glass panel opposite F.

each species alone. The control for these experiments consisted of a mixture of both species in the dark. Under the conditions of this experiment larvae of *D. melanogaster* tend to move away from the light and larvae of *D. willistoni* move toward light. When these species are placed together, the typical response of each species is intensified. A higher proportion of pupae of *D. melanogaster* are found away from the light source when *D. melanogaster* is raised in the same dish with *D. willistoni* than when larvae of *D. melanogaster* are alone. Likewise more larvae of *D. willistoni* move toward light when raised with *D. melanogaster* than when *D. willistoni* is alone. These changes in the distribution of pupae when the two species are placed together as compared to each species alone are statistically significant.

The results indicate that the larvae of different species of Drosophila have different preferences for light intensity. When two species are under interspecific competition (*D. melanogaster* and *D. willistoni*) the specific preference for light intensity becomes more pronounced than under intraspecific competition. Whether the competition is for food, space or any

other specific common requirement of the two species is not clear. The greatest competition between the two species for food or space would occur when both species are evenly distributed throughout the food dish, for example, the control dish in Experiment B. On the other hand interspecific competition for food is less intense when a differential distribution of the two species occurs due to responses to light intensity; intraspecific competition in this case will be increased. It seems possible that the intensification of response to light may be due to the tendency of larvae to move toward their optimal environmental conditions when disturbed by the presence of other species. The present results demonstrate that light is one of the environmental determinants of the degree of interspecific competition in Drosophila.

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SUMMARY

Larvae of *D. melanogaster* tend to pupate away from the light source whereas larvae of *D. willistoni* prefer relatively more illuminated areas for pupation. The respective responses to light intensity of these species are intensified when the two species are raised together. It is suggested that light intensity may serve as a factor determining the degree of interspecific competition of Drosophilae.

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LETTERS TO THE EDITORS

Correspondents alone are responsible for statements and opinions expressed. Letters are dated when received in the editorial office.

ON CROSSING-OVER AND SEX IN THE FOWL

In their recent note in this journal, Fisher and Landauer[1] take exception to my statement[2] that "Apparently crossing-over is influenced very little by sex in the fowl, at least so far as these figures for three different linkage groups can be any guide." They point out, with respect to crossing-over between creeper and rose comb, that the difference between the figure for females, 0.54 ± 0.07, and that for males, 0.24 ± 0.05 (probable errors), is statistically significant, with $P = < .03$. This was recognized in my statement that "Of these five cases, only one shows a statistically significant difference, and that is the rose comb-creeper pair."

The typographical error (to which they refer) in my table 63, by which a probable error was given as .70 instead of .07 was noted shortly after the book was published. It had no effect on my interpretation of the data.

While agreeing with Fisher and Landauer that the difference discussed above is statistically significant, I cannot agree with their assumption that it is, *ipso facto*, biologically significant. Some of the reasons for my doubts are evident in table 1, which gives, to the best of my knowledge, all the published data on crossing-over between creeper and rose comb. Other reasons will be found by careful reading of the original reports and even more convincing ones by attempting to classify the creeper mutant in dead embryos.

TABLE 1

CROSSING-OVER BETWEEN CREEPER AND ROSE COMB IN THE FOWL

	Crossing-over in females		Crossing-over in males	
	Gametes tested	Cross-overs per cent	Gametes tested	Cross-overs per cent
Serebrovsky and Petrov[3]	31	19.35	297	9.09
Landauer[4,5]				
In first year	2347	0.68	2136	0.19
In second year	1185	0.25	959	0.00
In third year	781	0.38	....	....
Taylor[6]				
In first year	501	1.60	198	4.04
In second year	683	0.59	1500	0.40

The point is that the cross-over values determined by different investigators, and those determined in different years by the same investigator,

are far too variable to permit much reliance on any statistical constants derived from lumped data. This is particularly so because the data include an unstated number of embryos, of age and size unspecified.

The remarkably high crossing-over given by Serebrovsky and Petrov[3] was ascribed by Landauer[4] to genetic differences in the Russian stock, but by Taylor[6] to inaccurate classification. Taylor found that the ratio of his two cross-over classes in his first year's data deviated so far from the equal numbers expected that some of his classifications must have been erroneous. In his second year's work, all chicks and embryos not easily classified were dissected for what proved to be more accurate identification. In my own experience, *Cp* is usually evident in hatched chicks, but sometimes difficult to recognize in embryos.

Considering Landauer's data, crossing-over in females was $0.68 \pm 0.17\%$ in the first year and $0.25 \pm 0.14\%$ in the second (standard errors). The difference between these values for the same sex in two successive years was 0.43 ± 0.22, which is greater than that between sexes on which Fisher and Landauer base their claim. The probability of getting such a difference by chance is only about .05. Can one say that .05 does not indicate a real difference, but that .03 does? When tests with 2,347 female gametes in one year cannot be verified with 1,185 in the next, can much significance be attached to very small differences between the sexes?

To Landauer's conclusion[5] that "With such a low frequency of crossing-over, it is difficult to obtain critical evidence for slight changes of crossing-over with age," one might well add that it is equally difficult to obtain critical evidence for slight differences attributable to sex.

Considering the risk of erroneous classification, and the fact that one error in 200 embryos could at least double the normal incidence of cross-overs, it would seem that the *Cp-R* linkage is hardly suitable for revealing sex differences in crossing-over. In the four other pairs of linked genes for which large numbers are available, no consistent or significant effect of sex is evident.[2]

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POSTERIOR GROWTH IN ANNELIDS

In an article in the May-June, 1953, number of this journal, Moment attributes to me the statement that earthworms continue to grow throughout life by the proliferation of new segments at the posterior end. What I actually said was (Hyman, 1940)[4] that chaetopod annelids grow in this manner. In making this statement I simply expressed general zoological knowledge. Anyone familiar with a variety of oligochaetes and polychaetes knows that they grow in this manner. It never occurred to me that it was necessary to produce any proof of something that has been incorporated into general zoological information. Stephenson (1930)[10] does not discuss the question of growth but limits himself to the following statement (page 3): "the growing zone, from which new segments originate, is normally situated just in front of the anus." Reisinger (1931)[9] (page 23) states: "Die Fähigkeit der Telomesoblasten ständig weiteres Mesoderm nach vorn hin abzugeben bedingt die Ausbildung der für die Anneliden-Körper so typischen, terminalen Wachstumzone." In the part on oligochaetes in the same volume, Michaelsen[8] declares (page 64): "Nur selten ist die Zunahme der Segmente mit Erreichung einer bestimmten, verhältnismässig geringen Zahl abgeschlossen." Probably, in fact, it never occurred to students of annelids to doubt the formation of new segments in front of the anal segment for at least a long time postnatally until Sun and Pratt (1931)[11] failed to find any evidence of such postnatal increase in segment number in what they called *Eisenia foetida*. Gates (1949)[1] considered that their data are unreliable because they confused four different species of Lumbricidae. Nevertheless, these authors raised an interesting question.

Moment in a succession of articles referred to in the article under discussion has proved that *Eisenia foetida* is hatched from the cocoon with the definitive number of segments. This may be true for the Lumbricidae in general. But the family Lumbricidae is only one of 14 families of oligochaetes and the most specialized and highly evolved family, at that. It is certain that in many oligochaete families, such as the Naididae, Tubificidae, Enchytraeidae, and Lumbriculidae, growth with posterior segment formation continues for at least long periods after hatching. Anyone can see this by examining the posterior end of such worms. *Tubifex tubifex*, one of the Tubificidae, hatches from the cocoon with about 30 segments, whereas the adult has around 150 segments (Hyman, 1916). Cultures of an enchytraeid are grown in this museum as food for small vertebrates. Ten of the smallest worms picked at random from these cultures containing thousands of worms had 24 to 37 segments whereas ten mature worms with a well-developed clitellum had 54 to 65 segments; what appeared to be newly hatched worms showed about 25 segments. Among polychaetes it is well known that the young worm often pauses for a time in the three-segment state and then, if sufficiently nourished, begins to add on new segments in front of the anal segment. Just (1922)[7] records that young *Platynereis* grew from the three-segmented condition to a state with 26 segments in

about two weeks. The length at that time was five mm. and in less than a year the length had increased to 60 mm. at which time sexual maturity had been attained. Just does not state the segment number at maturity, but from the literature it is easy to ascertain that this species at maturity has around 90 segments. Some young specimens of the fire worm, *Amphinome rostrata*, that I collected in the Bahamas showed an increase from 21 segments at a length of eight mm. to 27 segments at a length of twenty mm.; adults of this species have 64 segments at a length of 130 mm. It is really not open to doubt that the great majority of chaetopod annelids increase their segment number concomitant with growth.

It was shown by the Child school that chaetopod annelids have a U-shaped physiological gradient and this applies also to the potential differences along the axis[2,5,6] The two ends of such annelids (so far as tested) are electropositive to the middle. Leading off the potential from the two ends of the animal as was done by Moment therefore appears meaningless. The gradient, including the bioelectric component, appears similar in annelids that add on segments concomitant with growth and those that do not. I still adhere to the opinion expressed long ago (Hyman, 1918)[3] that intrinsic electrical gradients are a by-product of metabolic processes and not morphogenetic in themselves.

In view of the facts that most annelids add on segments indefinitely and that the electrical axial differences in these are similar to those in the few species born with the definitive number of segments, Moment's theory of growth would seem to be of very limited applicability.

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L. H. HYMAN

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PUBLICATIONS RECEIVED

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The genus Euglena is of especial interest in that it is a flagellate that belongs on the boundary between the plant and animal kingdoms. Both botanists and zoologists claim it. After a brief description of its morphology, and the necessary keys for its identification, Dr. Gojdics devotes the major portion of her book to the taxonomic description of some 155 species and varieties of it which are considered valid. This is followed by an annotated check list of all described species which are, in turn, illustrated by line drawings (about 275) printed clearly on the plates. The bibliography is copious and the index complete. This is a work which all students of the algae and the protozoa must consult.

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INDEX

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